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Population ecology of the five-lined skink, Eumeces fasciatus, at Point Pelee National Park, Canada.

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POPULATION ECOLOGY OF THE FIVE-LINED SKINK, *EUMECES FASCIATUS*, AT POINT PELEE NATIONAL PARK, CANADA

by

Carolyn Naomi Leff Seburn

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ABSTRACT

POPULATION ECOLOGY OF THE FIVE-LINED SKINK,

EUMECES FASCIATUS, AT POINT PELEE

NATIONAL PARK, CANADA

by

Carolyn Naomi Leff Seburn

The ecology of a population of five-lined skinks (Eumeces fasciatus) was examined at Point Pelee National Park, Ontario, Canada. Data were collected from April through September, 1989, using mark-recapture techniques. Location of animals, snout-vent length (svl), weight, head and tail width, and reproductive status were recorded. A total of 653 captures were made of 428 individuals at four sites in the park. Peak density of animals based on minimum number of animals alive ranged from 17-35 animals per hectare (not including hatchlings). Males were most abundant in May and June. Females peaked in abundance in August after the eggs hatched. Yearlings were significantly smaller (<58 mm svl) than adults until the end of June. Hatchlings were first seen August 2. Growth rates ranged from 0.6 (hatchlings) to zero (adults) mm svl per day. Adult sex was determined using discriminant functions analysis. Skinks were sexually dimorphic with males having wider heads and tails than females. Females were significantly heavier than males prior to oviposition and

significantly lighter afterwards. The weight of females remained depressed during the nesting period. Sex ratios were unbiased during the breeding period.

Individuals aggregated spatially within age and sex classes. Males and females significantly associated during the breeding period. A zero-truncated binomial was used to predict the expected number of animals captured only once by chance. Yearlings and males were significantly more likely to be non-resident than females. Age and sex classes did not differ for number of captures, residence time or catchability. Yearlings were found using twice as many microsites as adults. Artificial debris made up almost 50 per cent of microhabitat available to and used by the skinks. Average linkage cluster analysis of microsites based on surface area, thickness, shadedness and distance to nearest neighbour did little to reveal microhabitat preferences of skinks. Some females moved long distances (up to 68 m) before and after nesting. Nesting sites had greater surface area and harboured significantly more animals throughout the summer than other microsites. There was no evidence of territoriality.

DEDICATION

This work is dedicated to DCS without whose support, patience, love, and sense of humour, it could not have been completed, and to my parents who taught me to love knowledge.

ACKNOWLEDGEMENTS

Mike D'Asti, Linda Klassen and David Seburn provided invaluable assistance with the field work for this research. Drs. M'Closkey, Corkum, Starr, Weis and Ciborowski (University of Windsor) all put up with my numerous questions about statistical analysis and provided valuable advice. Drs. M'Closkey, Corkum, and Starr also suggested several improvements to this thesis. The University of Windsor Computing Consultants rescued me from the whims of computers on many occasions. David Seburn drew the figures and proofread several drafts of this thesis. The staff at Point Pelee National Park provided the impetus for this research and were helpful in many ways. Dr. Cooper (University of Auburn at Montgomery, Montgomery, Alabama) clarified many points of his own research for me. Steven Heenar provided data for the test of the discriminant functions analysis. I am grateful to all of them. I am especially grateful to Dr. M'Closkey for his encouragement and support.

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GENERAL INTRODUCTION

A major theme in the study of ecology is to delimit factors which influence the distribution and abundance of organisms. This theme may be addressed at a variety of spatial and temporal scales, from ecosystems to individual behaviour.

Carpenter (1967) suggested that most lizards demonstrate an awareness of space and of the boundaries of their home range, which results in territory defence. In such species, territoriality is associated with skewed sex ratios resulting from greater male mortality (Stamps, 1983). Territory size and the degree of polygyny are correlated because female home ranges tend not to overlap. Therefore males need larger territories to overlap with two or more females (Stamps, 1983). Polygyny, in turn is correlated with greater body size among males within species (M'Closkey *et al.* 1990b) and greater sexual size dimorphism between species (Stamps, 1983). These population level phenomena are associated with elaborate assertion and courtship displays. In captivity, territorial species often develop dominance hierarchies.

Lizards have been widely used as model organisms to test ecological theories (Milstead, 1967; Huey *et al.*, 1983). Members of the iguanid family, in particular, are well suited to these studies because of their intermediate position in the food web, small size, abundance, and easily observable behaviour. In addition, they are generally territorial and

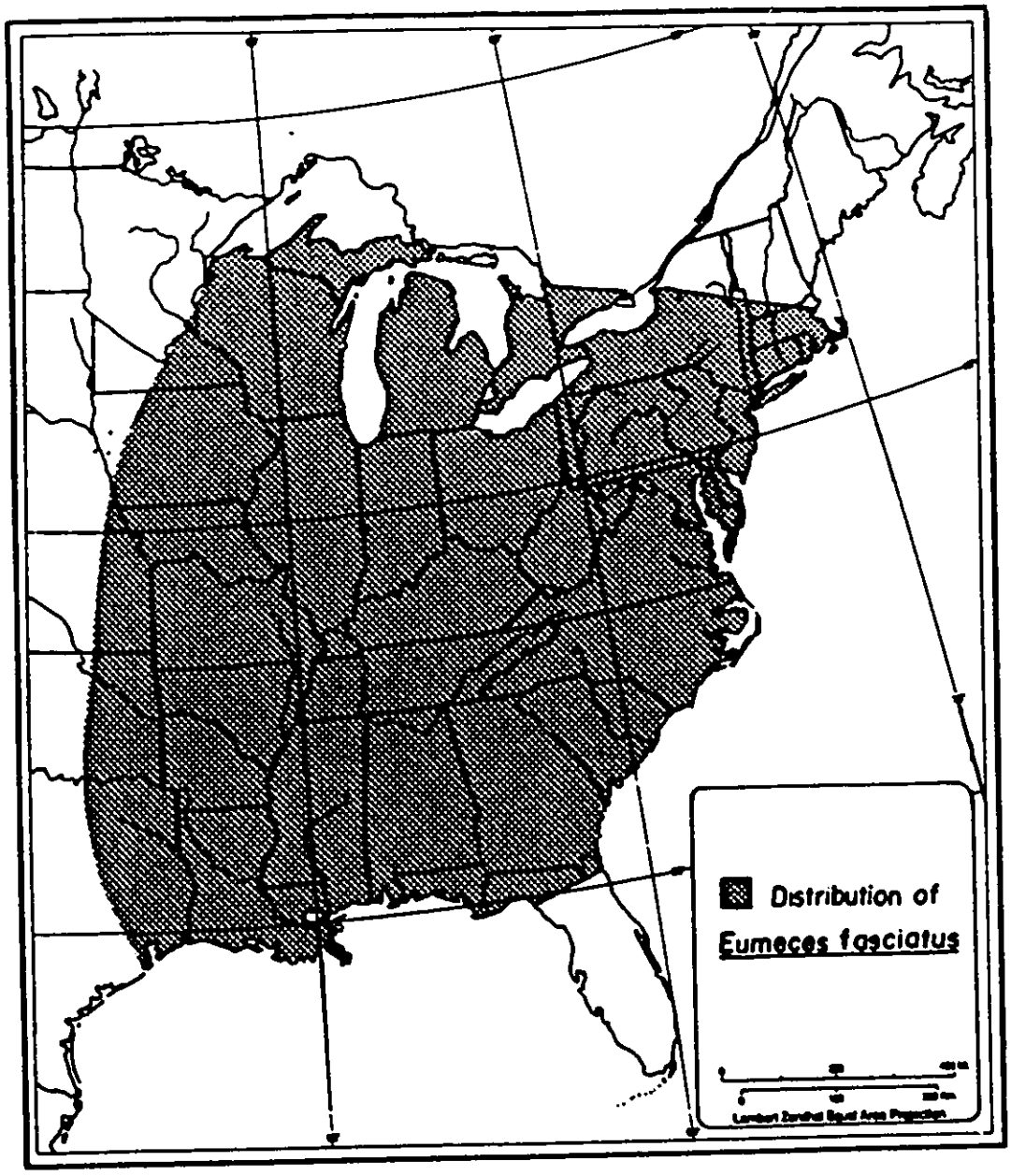
exhibit a wide range of mating systems and other social behaviours.

Lizards within the family Scincidae tend to be more difficult to study because of their secretive (even fossorial) behaviour. As a result, most manipulative studies have been done in the laboratory (Fitch, 1964; Clark and Hall, 1970; Cooper and Vitt, 1985a, 1987a, 1988; Cooper et al., 1986, 1987; Cooper and Garstka, 1987; Somma and Fawcett, 1989; but see Bustard, 1970 and Hasegawa, 1984). In spite of the difficulties, it is desirable that an effort be made to extend the lessons learned from iguanid lizards to other lizard groups, in order to test their generality.

Natural History of the Five-lined Skink, Eumeces fasciatus (Linneaus)

The five-lined skink, Eumeces fasciatus (Scincidae), a small insectivorous lizard, inhabits leaf litter and debris under open deciduous forest in eastern North America. Some populations also inhabit rocky outcrops (Seburn and Seburn, 1989). This skink ranges from northern Florida, U. S. A., to Georgian Bay, Ontario and as far west as Texas and the eastern border of South Dakota, U. S. A. (Fitch, 1954; Figure 1). Individuals reach sexual maturity by the start of their second summer and in extreme cases may live up to ten years (Fitch, 1956). Sexually mature males develop orange breeding colours on the head in spring. Breeding takes place once a

Figure 1. The distribution of Eumeces fasciatus in North America.


Distribution of
Eumeces fasciatus

year and one clutch of eggs is laid. Females attend the eggs until they hatch. Throughout the range, a large proportion of time is spent in hibernation.

Taylor (1936) first described the taxonomy of Eumeces, delineating fifteen groups of species within the genus. The Fasciatus group consists of twelve species all of which have, at birth, five light dorsal stripes on a dark background and a bright blue tail. This colouration pattern fades with age. Eumeces fasciatus is considered similar to the ancestral form. Two other members of the Fasciatus group are found in North America: E. laticeps, and E. inexpectatus.

Fitch (1954) described the life history of E. fasciatus based on a population in Kansas. Mechanisms of reproductive isolation among the three species have been described by Cooper and Vitt (1985b, 1986a,b,c, 1987b,c). Other research conducted on species within the genus Eumeces include studies of aggregation behaviour (Cooper and Garstka, 1987) and brooding behaviour (Noble and Mason, 1933; Hasegawa, 1984; Somma, 1985, 1987, 1988, 1989a,b; Somma and Fawcett, 1989).

Study Area: Point Pelee National Park, Canada

Point Pelee, a cuspate foreland, extends approximately 15 km into Lake Erie (Trenhaile and Dumala, 1978). It began forming about 4000 years ago (East, 1976) and is maintained by a combination of depositional and erosional processes (Trenhaile and Dumala, 1978). While erosional forces

dominate on the east side of the point, deposition causes the shoreline to advance, on average, 0.3 metres per year on the west side (Coakley, 1980). As a result various successional stages can be found on the west side of the point. In this research, I make a distinction between three stages of succession: unstabilized dune consisting of open sandy beach with little or no vegetation, stabilized dune characterized by a mixture of herbaceous vegetation with some shrubs and trees, and forest dominated by trees and shrubs.

The southern portion of the point was established as Point Pelee National Park in 1918. It is approximately 1564 hectares in size: 451 ha dry land, and 1113 ha marsh. The park's uniqueness is its diversity of plant and animal species. It has one of the last remnants of Carolinian forest in Canada and provides a staging ground for migrating birds and monarch butterflies.

Scope of Research

The current study aims to describe the pattern of abundance and spatial distribution of individuals within a population of five-lined skinks at Point Pelee National Park. In part one, I describe the population structure and examine how to differentiate yearlings from adults and females from males. Reproductive biology and hatchling recruitment are also described.

Part two compares these four segments of the population (male, female, yearling and hatchling). I examine spatial distribution, residence and movement patterns, catchability and related statistics, and microhabitat use.

Prior studies indicate that the five-lined skink is not territorial and that it is promiscuous (Fitch, 1954). Nonetheless, the skink is sexually dimorphic for head colour during the breeding period and other sexual differences may occur (Vitt and Cooper, 1986).

PART ONE

POPULATION STRUCTURE AND ABUNDANCE OF *EUMECES FASCIATUS*

Introduction

Population ecology focuses on the study of interactions among members of the same species. The magnitude of these interactions depends in part on the behaviour of individuals within the species, but is also influenced by the quality of the habitat and the density and structure of the population. For example, the patchiness of food resources may influence the degree of food territory defence (Brown, 1964), but this depends on population density and the feeding requirements of the species. Population density, which in turn varies with habitat quality, may also influence the degree to which polygyny is expressed (M'Closkey *et al.*, 1990b).

Sexual Dimorphism, Sexual Selection, and Mating Systems

The existence of differences between males and females of sexually reproducing dioecious species is a widespread phenomenon. Sexes have been found to differ on the basis of absolute body size (Darwin, 1871; Fitch, 1981; Shine, 1988) size of body parts (Vitt and Cooper, 1985) or weaponry (Geist and Bayer, 1988), physiology, colour (Cooper and Vitt, 1988), ornamentation (Raxworthy, 1989), behaviour (Emlen and Oring,

1977), life history (Kozlowski, 1989) and feeding ecology (Lups and Roper, 1988).

Darwin distinguished three distinct types of sexual differences. Primary sexual differences were related directly to the act of reproduction. Secondary sexual characters were involved in acquiring mating partners. Tertiary sex differences were "related to different habits of life" (Darwin, 1871). These definitions have the drawback of requiring that one know the evolutionary cause of the phenomenon before it can be named.

Darwin devised the theory of sexual selection to account for the existence of secondary sexual characteristics. Sexual selection could act in two distinct ways, either as a result of competition among males or as a result of female choice (Darwin, 1871; Emlen and Oring, 1977). Although female mate choice is more commonly studied, male mate choice has been found in at least two species of fish (Sargent et al., 1986). These two types of sexual selection may interact. In some cases they are concurrent as when females choose to mate with males that are successful competitors against other males (Howard, 1978a,b). However, in the stickleback, Gasterosteus aculeatus it was found that intra-sexual aggressiveness which is beneficial in acquiring territories is selected against in the context of mate acquisition (Ward and FitzGerald, 1987).

In polygynous populations, males should have greater

variance in reproductive success than females, if all females acquire a mate and some males acquire more mates than others. This increased variance is considered to be evidence of the operation of sexual selection, but Sutherland (1985) pointed out that this could occur by chance if males invest less time in mating than females do. Differences in investment time would likely be greater in polygynous species than in monogamous species.

It is commonly proposed that polygynous species should exhibit greater sexual dimorphism than monogamous species. Clutton-Brock (1983, p. 474) emphasized that "it is the comparative effects of phenotypic traits on reproductive success in males and females that will determine the degree of dimorphism and not the amount of variation in reproductive success per se". He suggested that the relationship between polygyny and sexual dimorphism was that reproductive success in males and females of monogamous species is likely to be determined by similar factors. In polygynous species it may be determined by different factors in males than in females.

Emlen and Oring (1977) suggested that the occurrence of sexual selection was dependent on the 'polygamy potential' of the environment. The polygamy potential resulted from an interaction between the temporal availability of mates and the spatial distribution of resources. Asynchrony in reproductive readiness of the female would lead to a male biased operational sex ratio, and some males would be

prevented from obtaining a mate. Clumping of resources or of females would make them economically defendable such that one male may attract or defend more than one female. The ability of a species to take advantage of the polygamy potential of the environment would depend on the degree to which offspring could be raised by a single parent.

Goals of This Study

I present data on the population density, size structure, and sex ratio in a population of five-lined skinks (Eumeces fasciatus) at Point Pelee National Park. The clear size structure of the population during late spring allowed the assignment of age class (yearling versus adult) to most individuals. Size structure during the second part of the summer allowed the assignment of age class to hatchlings (young of the year). Growth rates of size classes and sexes were determined and compared.

I describe the reproductive biology, including timing of events and estimates of hatchling recruitment. I quantified sexual dimorphism and classifed adults according to sex using discriminant functions analysis (Sokal, 1965).

Aside from colour dimorphism during the breeding period, I expected that adult males and females would differ for tail width (Taylor, 1936) and head width (Vitt and Cooper, 1986). Fitch (1954) found that males reached greater maximum body size (snout-vent length) than females but Vitt and Cooper

(1986) found no difference. Fitch (1954) found male-biased sex ratios which could lead to strong competition for mates but he also suggested that the mating system was promiscuous.

Is there any reason to expect sexual selection to occur in this species? Trivers (1972) suggested that differences in parental investment of the sexes should lead to sexual selection because the sex which invests more will be more limited in its reproductive potential and therefore will act as a limiting resource for the other sex. Aside from carrying unlaid eggs, Eumeces fasciatus females brood their eggs (Noble and Mason, 1933; Somma, 1990) for up to 47 days (Fitch, 1954) and there is no evidence that male E. fasciatus contribute any parental care. In order to examine this idea, I recorded the number of times females were found on their nests and whether males were associated with nesting females.

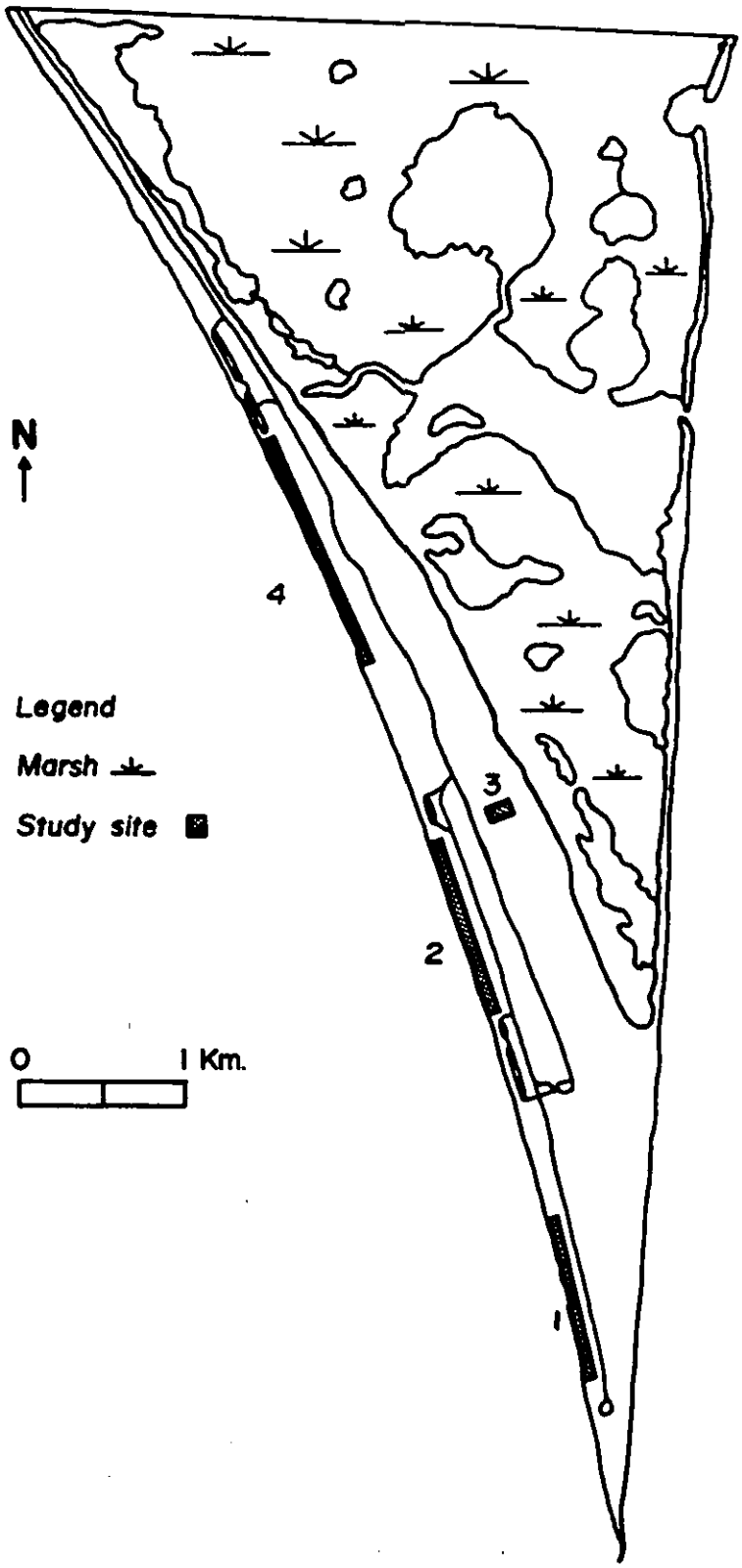
Methods

Field Methods

In the initial census, all areas of Point Pelee that appeared to have suitable habitat were censused. The marsh and the thickest part of the forest were excluded. Four study sites were selected (Figure 2) in areas where the greatest number of animals were caught. Three of these areas extended approximately one km in length along the west side of the park. Width of the sites varied depending on the location of the forest edge. These sites were subdivided into subsites 100 metres in length (50 metres in site one). I chose these sites because successful captures were made in those areas and because they differed somewhat in the amount and size of established vegetation. Site one was heavily wooded with occasional small clearings. Site two had fewer trees and larger clearings. Site four consisted of open meadows separated by small clumps of mature willows (Salix nigra) and poplars (Populus deltoides) with associated smaller trees. Site three included an area around the Warden's station where building materials and scrap lumber were stored or discarded.

I censused these four sites six times between April 28 and June 22. Time constraints forced a reduction of the area of study to eight subsites chosen on the basis of a high density of animals. Four subsites in site two (A, B, C, and D) were chosen, each about 1000 m^2. Subsites A, B, and C

Figure 2. Location of study sites in Point Pelee National Park, Ontario, Canada.


N
4
3
2
1
Legend
Marsh
Study site
0
1 Km.

were contiguous. Subsite D was approximately 450 metres south of subsite C. I censused these subsites an additional 16 times between June 22 and September 24. Subsites A, B, C and D in site four were 2560, 1200, 1200 and 1500 m^2, respectively. None of these subsites were contiguous. Each was censused an additional nine times between June 22 and August 14 (Table 1). Site four was abandoned after August 14 because of a high level of human disturbance. Each census consisted of thoroughly searching and turning logs, boards and drift wood. Animals were captured by hand. Animals captured for the first time were given a unique toe-clip (no more than one toe-clip per foot). In warm weather a census began at first light and ceased when warming allowed several consecutively sighted animals to escape capture. I recorded snout-vent length (svl, mm), head width (mm), tail width (mm), weight (g), head colour, tail colour, tail condition and location of capture. Head width was measured at the widest part of the head which coincided with a line drawn through the dorsal edge of the parietal scales. Tail width was measured at the vent. Both head and tail widths were measured using vernier scaled calipers.

A bias of unknown magnitude resulted from occasional disturbances of the study sites. Some of these were likely due to patrons of the park unknowingly disturbing microsites or searching for animals and not replacing microsites properly. However, on one occasion (July 25, 1989) the

Table 1. Summary of census data.

CENSUS CATEGORY	SITE ONE	TWO	THREE	FOUR
Number of Censuses	6	21	6	15
Adult males marked	29	30	10	36
Adult male recaptures	6	24	7	25
Adult females marked	13	45	5	22
Adult female recaptures	8	67	5	23
Yearlings marked	12	31	15	26
Yearling recaptures	13	25	7	7
Hatchlings marked	---	89	---	20
Hatchling recaptures	---	35	---	0
Total marked	64	214	30	120
Total recaptures	28	121	19	57
Total captures	92	335	49	177

disturbances coincided with the disappearance of four clutches of eggs suggesting that some poaching of skinks took place. Further thorough disturbances in spring, 1990, suggest that poaching is a greater problem then previously suspected, but there is no way of estimating how many animals have been removed or how this study has been affected.

Data from all four sites entered into the analysis of growth rates and the size distribution. The four sites were compared on the basis of sex ratios. Other analyses were conducted separately on data from sites two and four.

Weights were measured using a Pesola 50 g scale for adults and a Pesola 10 g scale for hatchlings. Both scales were precise to 0.2 grams. At the end of the summer, the Pesola 50 g scale was found to have been consistently inaccurate and was calibrated against standard brass weights (Appendix A).

No reliable external indicator of sex could be found. Females tend to retain juvenile colouration longer than males do but this is highly variable. However, males could easily be identified by their breeding colours in the spring. At this time they develop a bright orange suffusion of the jaws and chin. I considered it important, however, not to rule out the possibility of cryptic males -- males that looked like females. Initially animals were categorized as male and female only if this categorization was absolutely certain. Females were identified on the basis of brooding behaviour.

Comparison of weight changes in known males and females allowed the development of a decision rule for identifying gravid females, but could only be applied to animals captured more than once. Only animals > 60 mm svl at first capture were included in the study of sexual dimorphism.

Quantitative and Statistical Methods

Several variables were derived from the raw data and used in the analyses described below. Population sizes were estimated using two different methods, the Jolly-Seber method and the minimum number alive method. The sex of adults was determined by discriminant functions analysis. These determinations were used to calculate a sex ratio for each site. Age class (yearling versus adult) was assigned based on the frequency distribution of size (svl) classes. Growth rate was estimated by the slope from a regression of svl on date of capture for each animal captured more than once.

The Jolly-Seber method is commonly used to estimate the size of open populations where multiple mark-release census data are available (Southwood, 1978). Explicit assumptions of the method include short census time relative to the interval between censuses, and equal and constant catchability of all members of the population. When the total number of animals captured varies from census to census the variance of the estimates may produce inconsistent results. An additional assumption is that captured animals

mix thoroughly with uncaught animals between censuses.

Estimates of minimum number alive (M'Closkey et al., 1990a) were less sensitive to random fluctuations in the number of animals captured and were therefore used in estimates of age and sex ratio. Minimum number alive was also used to estimate peak density although it is biased to produce a minimum estimate.

The Goodness-of-fit-test (Sokal and Rohlf, 1981) was used to determine the degree to which data fit an expected distribution. Sex ratios were compared to a 1:1 distribution. In all cases where a G-test was used, Williams' correction for continuity has been applied (Sokal and Rohlf, 1981).

An analysis of covariance (ancova) compared growth rates in different segments of the population, using initial svl as the covariate. Outliers were removed by applying Grubb's method (Sokal and Rohlf, 1981) to the residuals of a regression of the data against initial svl.

Distributions of svl, weight, head width and tail width for known males and females were tested for normality and heteroscedasticity. The Shapiro-Wilk W statistic (SAS™ Institute Inc., 1985 b) was used for testing normality of samples with sample size less than 50. For samples larger than 50, the Kolomogorov D statistic was used. Bartlett's test of homogeneity of variances (Sokal and Rohlf, 1981) was

used in comparing the two distributions. These analyses made use of measurements taken during the first capture of each animal.

Multivariate analyses of variance (manova) were used to compare known males and females using svl, weight, head width and tail width. These manova were calculated using data from two time periods: last capture prior to July 6 (beginning of oviposition) and first capture after July 22 (the end of oviposition).

Known males and females were entered into a discriminant functions analysis using svl, weight, head width and tail width (Sokal, 1972). The resulting functions were applied to adults of unknown sex who were then classified on this basis. Separate analyses were conducted for last captures of animals prior to oviposition and first captures of animals after oviposition. The validity of the discriminant functions analysis was tested using data on animals of known sex captured at Point Pelee in 1990. Sex of yearlings and hatchlings could not be determined.

Analyses of frequencies were carried out on an IBM PC using programs written by Sokal and Rohlf (1981) or by Krebs (1989). Analyses of variance, regressions and the discriminant functions analyses were performed on a CMS system using the SAS™ statistical package (SAS™ Institute Inc. 1985 a,b). Scheffe's multiple comparison test (Dunn and Clark, 1987) was used to differentiate three or more means.

Results

Population estimates

Two methods were used to estimate population sizes: the Jolly-Seber (Jolly, 1965; Southwood, 1978) method and the minimum number of animals known to be alive (mna). These estimates were significantly correlated ($p < 0.0001$) at site two ($r^2 = 0.51$) and at site four ($r^2 = 0.79$; Tables 2 and 3). Recapture rates ranged from 48 per cent in May to 75 per cent in August (excluding hatchlings). Density of animals at each subsite refers to the peak number of animals per hectare based on estimates of mna (Table 4). Hatchlings were not included in estimates of population size or density.

The abundance of age and sex classes varied over time (Figures 3 and 4). In site two, male numbers increased to a maximum in May and dropped steadily through the summer. Females actually peaked in August after hatchlings had appeared. Yearling numbers peaked in June and dropped rapidly through the summer. In August and September, hatchlings made up the bulk of the population. At site four, males, females and yearlings were at maximum in June and dropped through the summer. Hatchlings are not included because there were not enough censuses for an accurate measurement of hatchling numbers. Overall, yearlings made up 33 per cent of the population (exclusive of hatchlings). Hatchlings increased the population size by 114 per cent.

Table 2. Correlation between minimum number alive (mna) and Jolly-Seber estimates at site two.

CENSUS	DATE	MNA	JOLLY-SEBER
2	MAY 16	27	30.8
3	MAY 39	28	94.3
4	JUNE 6	32	72.7
5	JUNE 15	30	65.7
6	JUNE 22	33	102.6
7	JULY 3	31	81.2
8	JULY 6	26	64.4
9	JULY 12	30	50.1
10	JULY 17	29	65.3
11	JULY 18	26	34.1
12	JULY 22	24	73.2
13	JULY 25	23	57.3
14	AUG. 2	23	48.2
15	AUG. 3	19	45.0
16	AUG. 10	23	42.0
17	AUG. 14	24	43.9
18	AUG. 18	22	39.9
19	AUG. 26	17	41.1
20	SEPT. 4	9	15.0

$r^2 = .51$ $p < 0.001$

Table 3. Correlation between minimum number alive (mna) and Jolly-Seber estimates at site four.

CENSUS	DATE	MNA	JOLLY-SEBER
2	MAY 23	14	16.0
3	MAY 31	13	17.1
4	JUNE 8	15	29.0
5	JUNE 12	16	24.0
6	JUNE 19	18	58.0
7	JUNE 30	13	11.3
8	JULY 5	15	13.9
9	JULY 13	13	9.9

$r^2 = .79$ $p < 0.005$

Table 4. Density of animals at each subsite. Total number of males (M), females (F), adults of unknown sex (U), yearlings (Y) and hatchlings (H) captured.

SUBSITE	PEAK DENSITY PER HECTARE	TOTAL NUMBER CAPTURED					TOTAL/HA (EXC. H)
		M	F	U	Y	H	
2 A	27.5	6	10	0	9	14	62.5
2 B	17.5	6	4	0	3	30	32.5
2 C	22.5	6	6	0	7	8	47.5
2 D	30.0	6	11	0	6	38	55.0
4 A	27.3	2	3	1	6	8	46.9
4 B	33.3	5	2	0	3	1	83.3
4 C	41.7	3	7	2	7	7	158.3
4 D	53.3	3	3	1	1	1	53.3

Figure 3. Minimum number of males (solid), females (dashed), yearlings (dotted) and hatchings (dot-dash) known to be alive at site two (subsites A, B, C, and D).

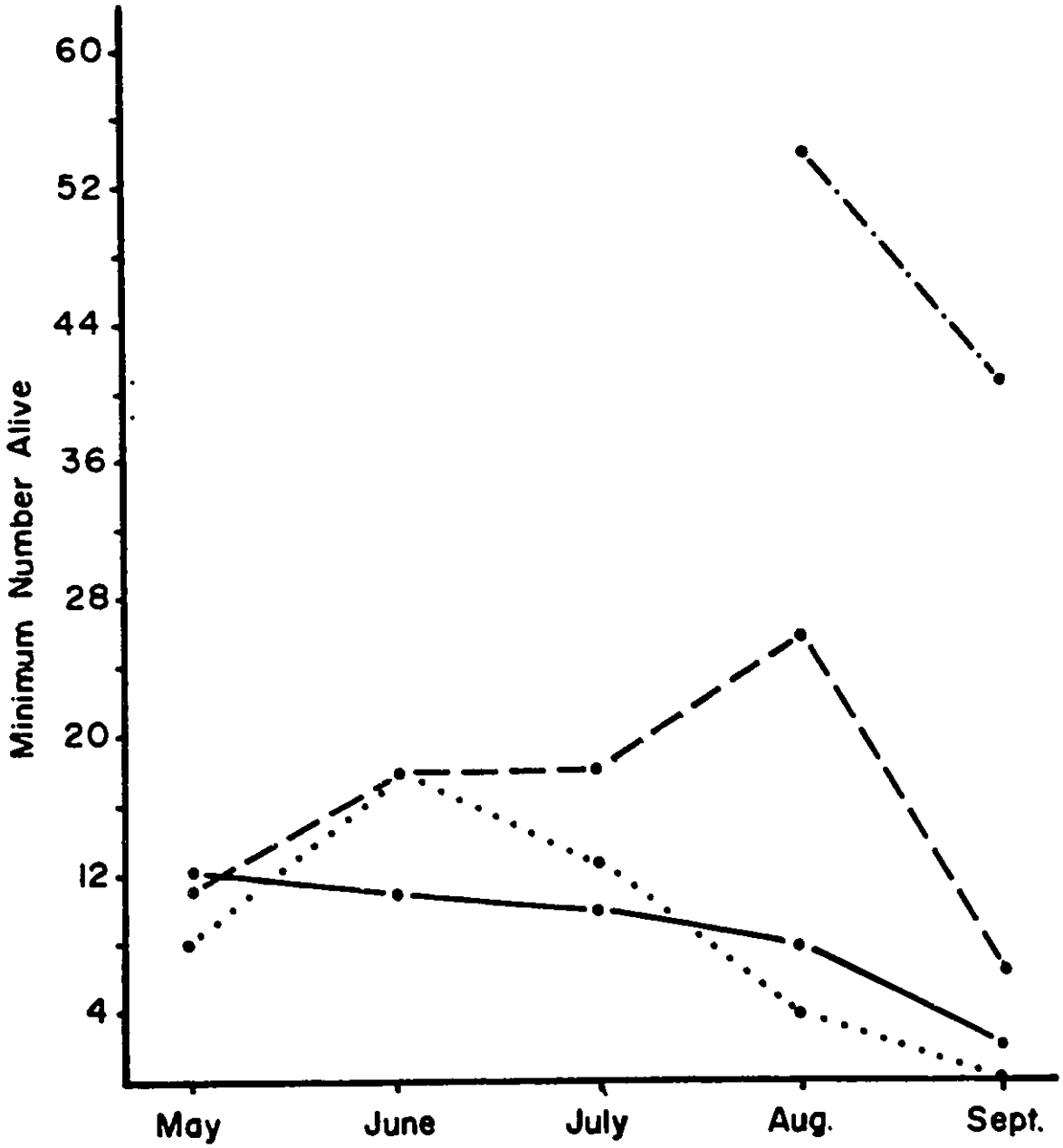
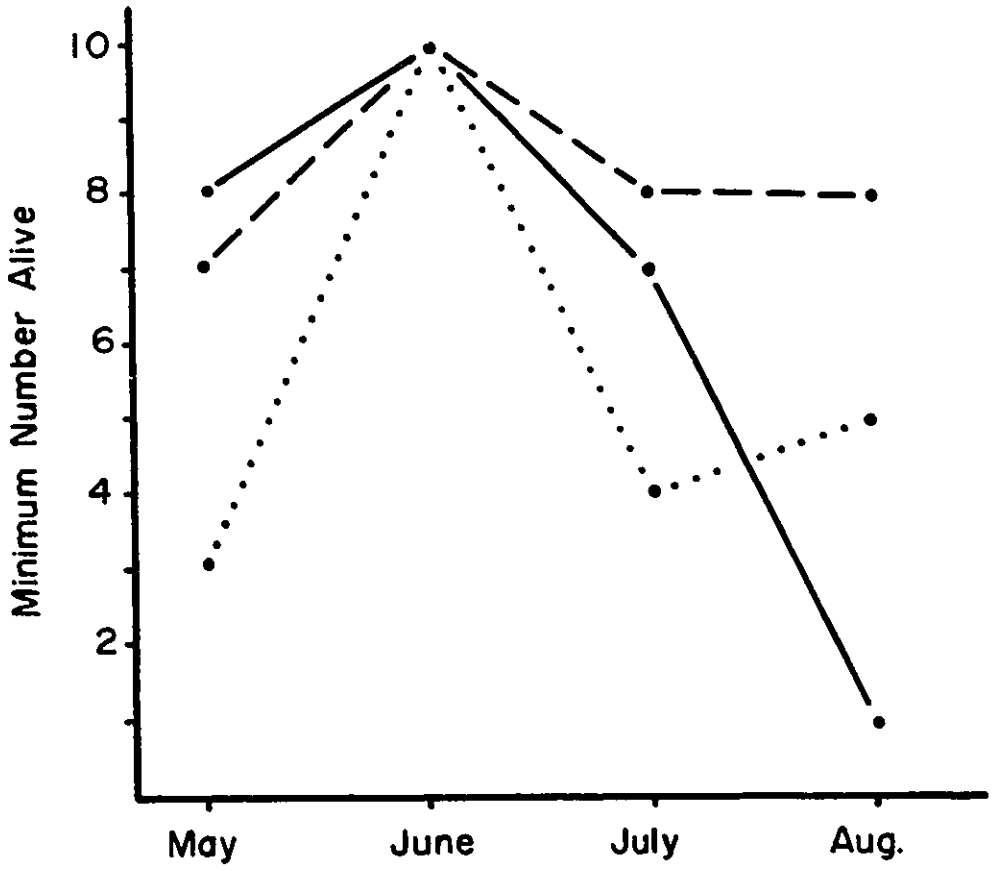

Minimum Number Alive
60
52
44
36
28
20
12
4
May
June
July
Aug.
Sept.

Figure 4. Minimum number of males (solid), females (dashed), and yearlings (dotted) known to be alive at site four (subsites A, B, C and D).

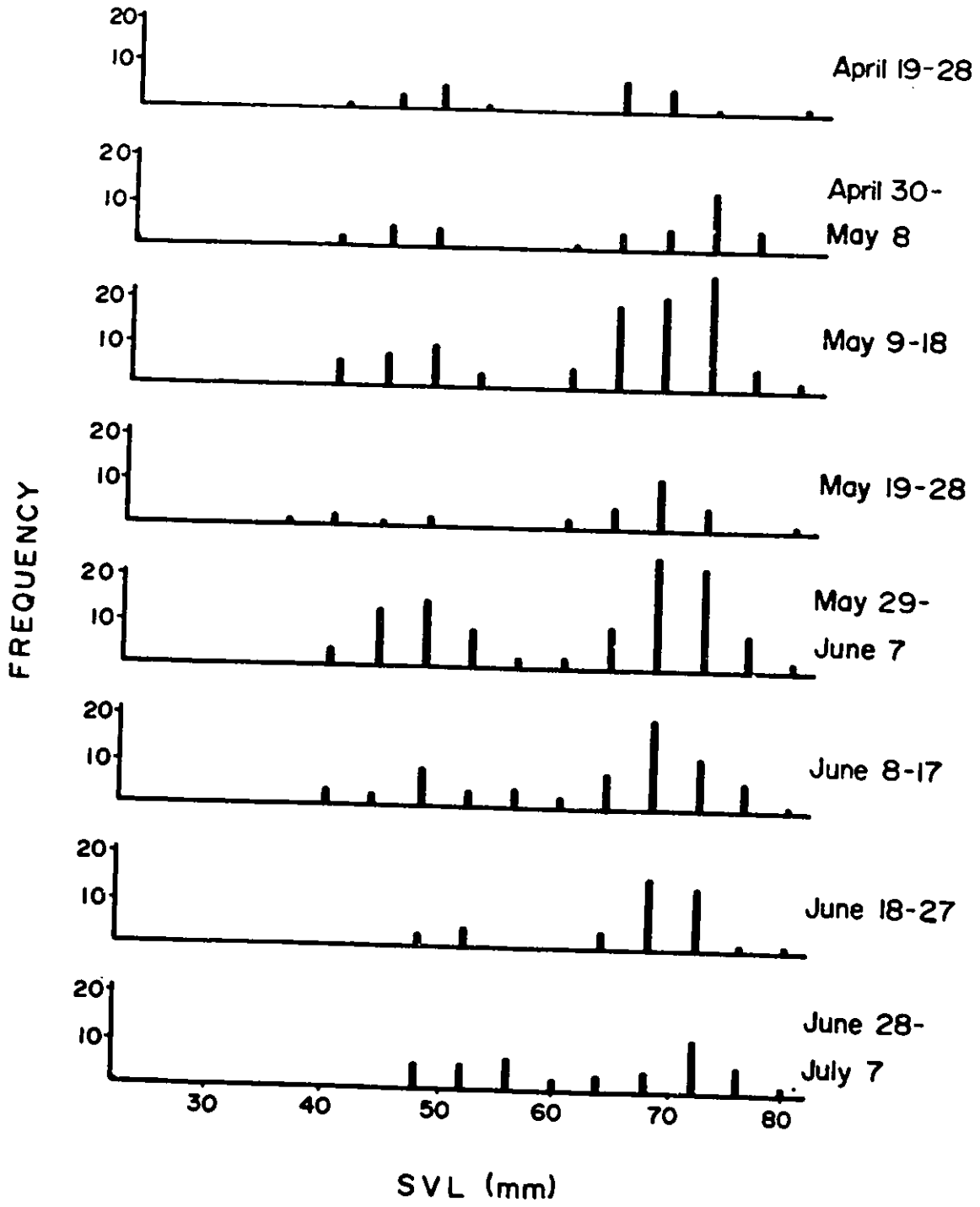

Minimum Number Alive
10
8
6
4
2
May
June
July
Aug.

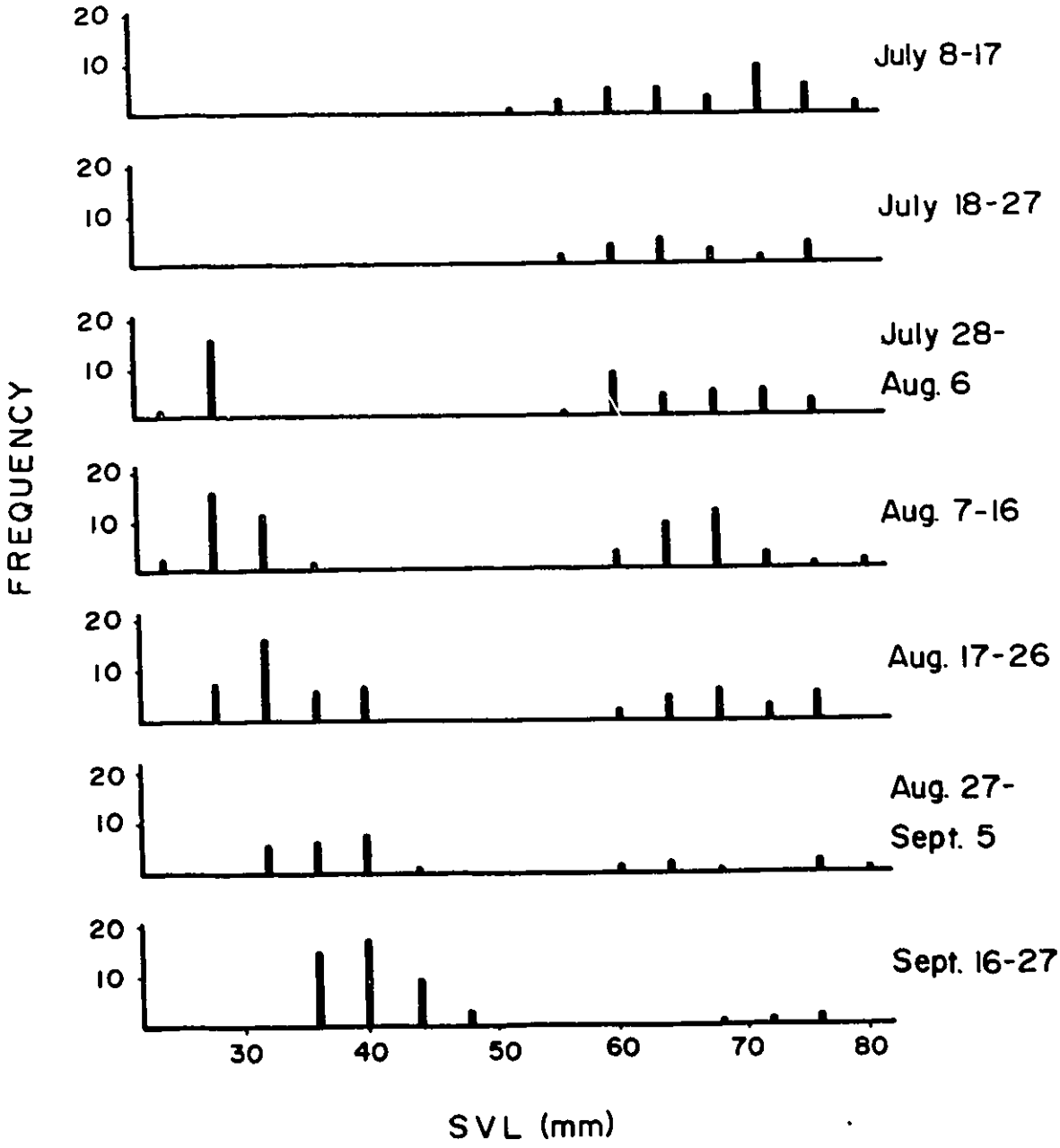
Changes in relative abundance of different age classes and growth of individuals resulted in seasonal changes in the size distribution of animals. Frequency distributions of size classes for each ten-day period throughout the summer (Figure 5) show that in the spring and continuing until the end of June, yearlings can easily be distinguished from adults on the basis of svl alone. After June there is no clear-cut difference. However, of 42 yearlings only a small number of animals were newly captured after June and so only nine animals could not be classified to age class. Hatchlings appear as a second mode at the beginning of August and remain distinct through the end of the season. These results are based on animals captured at all study sites.

Growth Rate

Least squares regression of svl on date of capture determined growth rates of each individual captured more than once. Because of the small number of captures per animal (maximum 8, average 1.38) these regression lines did not, in general, have significant slopes. This was not unexpected and the slopes of the regression lines were taken to be estimates of growth rate (mm/day). Some negative growth rates were found and resulted from random errors in the measurement of svl. These errors occurred because the animal attempts to curve its body while the measurements were made.

Figure 5. Distribution of size classes for ten-day periods throughout the summer, 1989.


20
10
April 19-28
April 30-
May 8
May 9-18
May 19-28
May 29-
June 7
June 8-17
June 18-27
June 28-
July 7
FREQUENCY
30
40
50
60
70
80
SVL (mm)


FREQUENCY
20
10
July 8-17
July 18-27
July 28-
Aug. 6
Aug. 7-16
Aug. 17-26
Aug. 27-
Sept. 5
Sept. 16-27
30
40
50
60
70
80
SVL (mm)

The range of growth rates found for each segment of the population were as follows: hatchlings, -0.33 to 1.0 (0.05 to 0.60); yearlings, -0.54 to 0.5; adult females, -0.67 to 0.60 (-0.35 to 0.50), adult males, -0.56 to 0.35 (-0.39 to 0.35). Bracketed ranges are based on data with outliers removed.

Outliers, in each segment of the population, were identified by examining the residuals of a regression of growth rate on initial svl. These residuals were tested for normality and potential outliers were located by examination of quartile-quartile plots and were tested for significance by Grubb's method (Sokal and Rohlf, 1981). The residuals for yearlings were normally distributed and so no attempt was made to find yearling outliers. One outlier was identified at the upper end of the distribution of males and for symmetry the lowest value of that distribution was also removed. Similarly two outliers were removed from the distribution of females. The two outliers identified from the hatchling distribution were at opposite ends of the distribution and both were removed. The hatchling distribution remained marginally leptokurtic but removal of further outliers would have led to heterogenous variances. All outliers resulted from paired svl measurements fewer than ten days apart.

Using these trimmed data, four segments of the population, adult males and females, yearlings and hatchlings

were compared for growth rate using initial svl as a covariate. The variance in growth rate was homogenous among groups ($F = 2.59$, $p > 0.05$) and therefore an analysis of covariance (ancova) was conducted. The outcome was essentially the same when number of captures was used to weight the data and therefore only the results for the unweighted calculations are reported (Table 5). Segments of the population differ significantly for growth rate ($F = 9.64$, $p < 0.0001$) but not when svl is used as a covariate ($F = 0.58$, $p > 0.63$). Within segments the effect of svl is significant ($F = 10.09$, $p = .0019$). Clearly growth rate decreases with increasing size (Figure 6).

Reproductive Biology

During the breeding period, males developed bright orange colouration about the jaws and chin. Traces of this colouration were seen on some males throughout the summer but the peak intensity lasted for two weeks (May 25 to June 8; Table 6). Ninety-seven animals (15 yearlings and 82 adults) were captured with some degree of orange colour.

Of 69 males captured prior to oviposition time, 28 were captured with a female at least once. There were no significant differences between males captured with and without females for svl ($F = 1.98$, $p = 0.17$), weight ($F = 1.68$, $p = 0.2$), head width ($F = 1.68$, $p = 0.2$) or tail width at the vent ($F = 0.29$, $p = 0.6$).

Table 5. Analysis of growth rate (mm/day) in males, females, yearlings and hatchlings, with initial svl as a covariate. Means with different superscript letters differ significantly (Scheffe's multiple comparison, $p < 0.05$).

	MALES	FEMALES	YEARLINGS	HATCHLINGS
$\bar{X}$	0.0151^a	0.0791^a	0.1771^b	0.2640^b
S^2	0.0204	0.0227	0.0339	0.0131
n	35	49	30	23
ANCOVA				
F	9.64		p	< 0.0001

Figure 6. Growth rate as a function of initial snout-vent length in males, females, yearlings and hatchlings.

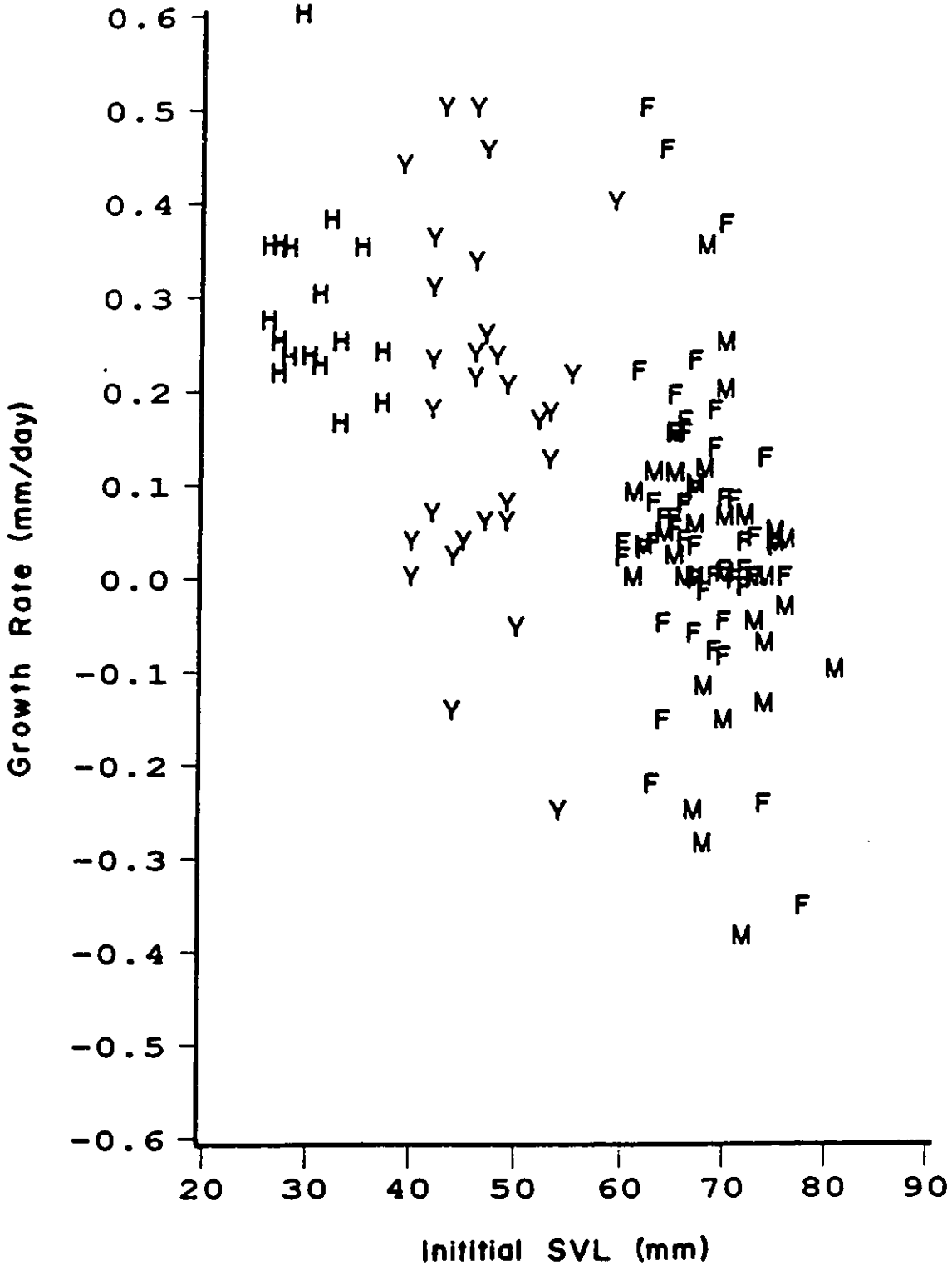

Growth Rate (mm/day)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
20
30
40
50
60
70
80
90
Inititial SVL (mm)

Table 6. The timing of reproductive events. Where uncertainty exists due to lack of data, maximal time periods are assumed.

TIME PERIOD	EVENT
April 15 - 30	General emergence from hibernation
April 28 - May 25	Males developed breeding colours
May 25 - June 8	Peak of male breeding colours
June 8 - July 17	Females were gravid
July 12 - July 17	Females oviposited
July 12 - Aug. 5	Females brooded
July 26 - Aug. 5	Eggs hatched
Aug. 25 - Sept. 16	General disappearance of adults
Sept. 30	Last visit, one adult, several hatchlings seen

The first gravid female was captured June 8. The largest weight change found between the last gravid capture and first brooding capture was 5.4 g. Females laid one clutch of eggs which they brooded in nest chambers until the eggs hatched. Thirteen females were captured while brooding eggs. The smallest of these was 59 mm svl. Clutch sizes ranged from five to thirteen eggs excluding one female with 21 eggs. This female was captured with two other females, one of whom was brooding eight eggs and the other behaving as if she were brooding but having no eggs. Assuming that this last female was the mother of some of these 21 eggs, the average clutch size was 9.36. Number of eggs was not significantly correlated with svl ($r^2 = 0.05$, $p > 0.1$).

Nests consisted of shallow depressions under logs and boards or inside logs. It is assumed that most nests located inside logs were not found because no attempt was made to open intact logs. On only two occasions was a nest found unattended. Egg length just prior to hatching ranged from 12.2 to 13.9 mm (average 13.2, n = 12).

For a few days after hatching neonates appeared translucent on the ventral surface and had a small amount of yolk still attached. Shedding the skin often occurred within the first few days. Initial svl was 25 - 28 mm (average 27.3 mm, n=7).

In site two, I captured 19 gravid or brooding females and 19 adult males with breeding colours. Hatchling captures numbered 82 or about 4 hatchlings per gravid female or breeding male. Estimates of hatchling numbers based on the Jolly-Seber method and the minimum number alive method were not correlated (Table 7).

Sexual Dimorphism

Females could be positively identified if captured while brooding eggs. To increase the sample of known females it was necessary to verify the subjective determination of gravid animals by examining changes in weight before and after oviposition time for known adult males and females (Figure 7). Six of the brooding females were captured both before and after oviposition. All of these animals gained significant amounts of weight prior to oviposition and lost weight during oviposition. Of 29 males captured more than once, 14 lost weight prior to the time of oviposition, 14 gained not more than 0.02 g/mm svl and one remained unchanged. All males gained weight during the time of oviposition and thereafter.

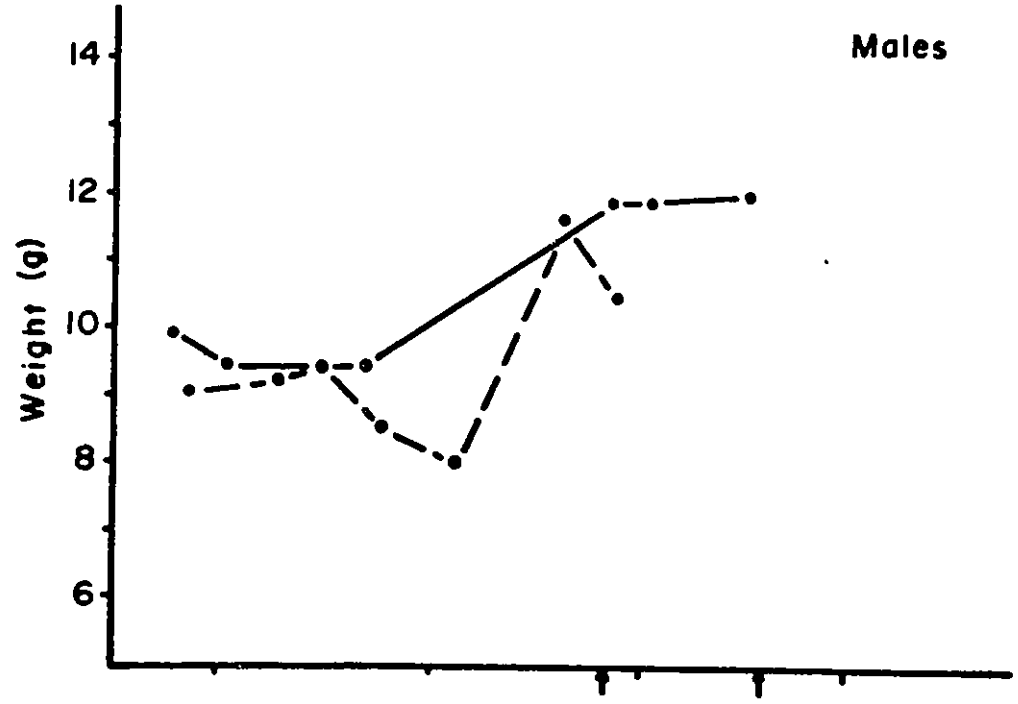
Based on these results a decision rule was devised and applied to all adults captured more than once: designate as female if weight/svl increased by 0.03 g/mm svl or more prior to oviposition or decreased by 0.01 g/mm svl or more during oviposition. Twenty-two additional females were classified.

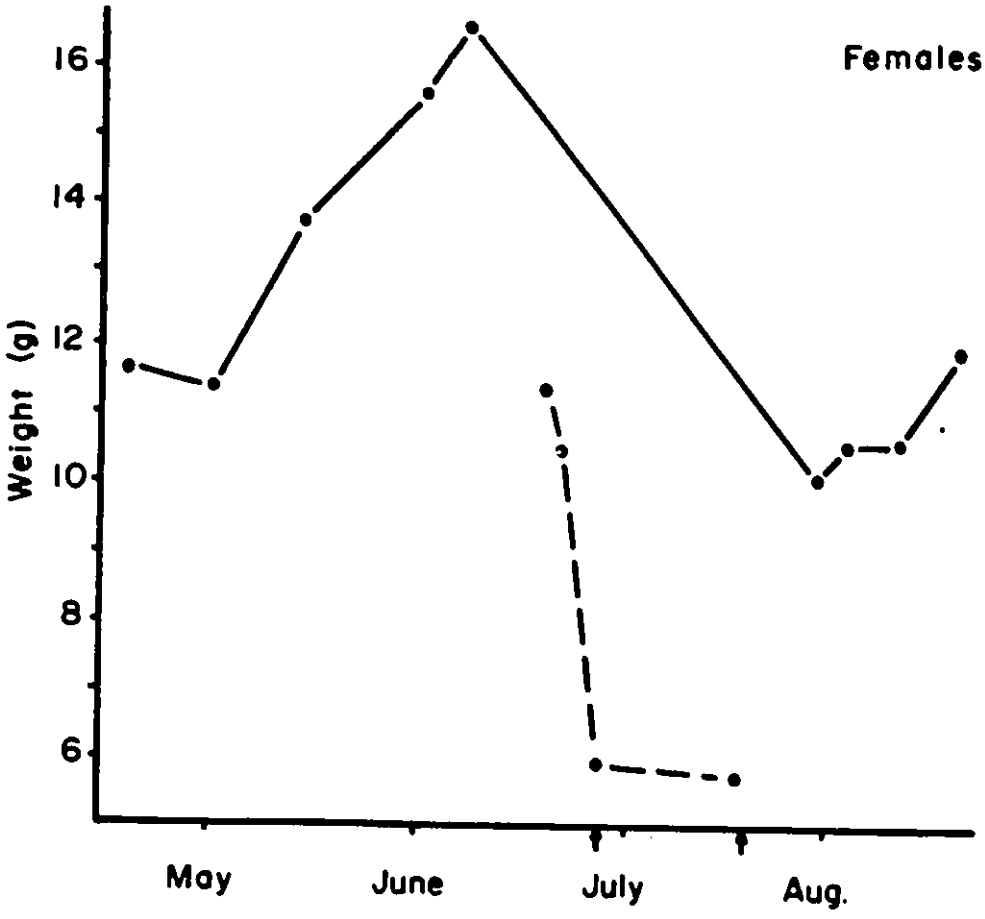
Table 7. Correlation between minimum number alive and Jolly-Seber estimates of hatchling numbers.

CENSUS	DATE	MNA	JOLLY-SEBER
2	AUG. 10	8	49.0
3	AUG. 14	15	30.0
4	AUG. 18	29	218.4
5	AUG. 26	24	83.6
6	SEPT. 4	30	64.0
7	SEPT. 16	28	67.0

$r^2 = 0.26$ $p > 0.05$

Figure 7. Weight (g) as a function of time (days) for four typical adult skinks. Male #65 (solid line) and male #109 (dashed line) were initially 70 and 63 mm svl, respectively (top). Female #35 (solid line) and female #111 (dashed line) were initially 75 and 66 mm svl, respectively (bottom). The first arrow indicates oviposition. The second arrow indicates hatching.


Males
Weight (g)
14
12
10
8
6


Females
Weight (g)
16
14
12
10
8
6
May
June
July
Aug.

There were 29 known females and 69 known males captured prior to oviposition. After oviposition, there were ten known females and nine known males. Nine of these animals had been included in the before oviposition group as well. Known males and females were compared using two data bases (last captures before oviposition and first captures after oviposition) and using manova on svl, weight, head width and tail width (Tables 8, 9).

Data on known males and females were entered into discriminant functions analyses. There was 100 per cent correspondence between prior and posterior classification. The discriminant functions based on captures prior to oviposition (Table 10) were then applied to 98 adults of unknown sex, captured before oviposition. All classifications with a posterior probability of 75 per cent or better were accepted. In this way, 91 of the 98 adults were classified leading to 40 new females and 51 new males.

The discriminant functions based on captures after oviposition (Table 10), when applied to 29 adults of unknown sex, classified them as 28 females and one male. All classifications had a probability greater than 96 percent. Four of these animals were captured before oviposition as well. Three were classified the same by both analyses. The fourth was classified in the first group as male with $p = 0.6$ and in the second group as female with $p = 1.0$.

Table 8. Comparison of known males and females captured prior to oviposition. Based on the 27 females and 70 males entered in the discriminant functions analysis.

	SVL (mm)	WEIGHT (g)	HEAD WIDTH (mm)	TAIL WIDTH (mm)
MALES	70.5	9.68	11.96	9.58
FEMALES	70.4	11.61	9.58	6.33
MANOVA				
F	0.02	14.08	80.00	19.21
p	0.8999	0.0003	0.0001	0.0001

OVERALL F = 72.88 p = 0.0001

Table 9. Comparison of known males and females captured after oviposition. Based on the 10 females and 9 males entered in the discriminant functions analysis.

	SVL (mm)	WEIGHT (g)	HEAD WIDTH (mm)	TAIL WIDTH (mm)
MALES	72.7	11.8	12.46	7.42
FEMALES	67.5	7.86	9.66	6.17
MANOVA				
F	5.53	21.50	68.47	10.84
p	0.0310	0.0002	0.0001	0.0043

OVERALL F = 27.72 p = 0.0001

Table 10. Discriminant function based on known males and females before and after oviposition.

	BEFORE	AFTER
CONSTANT	55.816	88.267
SVL	0.463	-0.847
WEIGHT	-3.747	-0.600
HEAD WIDTH	5.418	15.543
TAIL WIDTH	0.696	-0.222

When the discriminant functions were applied to data from sixteen adults of known sex captured at Point Pelee in 1990 there was again 100 per cent correspondence between prior and posterior classification (Table 11).

Sex Ratios

Sites were used as replicates to test whether sex ratios differed significantly from 0.5 (Table 12). A G statistic tested the significance of bias in the sex ratios. Within each site, all captures throughout the summer were lumped initially. Only site one had a significantly biased sex ratio and as a result sites were not homogeneous (H_1). When data for all sites were pooled they did not reveal a significantly biased sex ratio (H_2). However, the bias in site one was sufficiently large that the total G (sum of heterogenaity G and pooled G) is significant (H_3).

Sites one and three were only censused in May and June but sites two (subsites A, B, C, and D) and four (subsites A, B, C and D) were further tested by determining if the sex ratio varied over the season. At both sites (Tables 13 and 14) the sex ratio only deviated significantly from 0.5 during August.

Table 11. Results of applying discriminant functions to sixteen adults of known sex captured at Point Pelee in 1990. The first fourteen were captured prior to oviposition. The last two were captured after oviposition.

ANIMAL	KNOWN SEX	CLASSIFICATION	PROBABILITY
1	MALE	MALE	0.9999
2	FEMALE	FEMALE	0.9999
3	MALE	MALE	0.9183
4	FEMALE	FEMALE	1.0000
5	MALE	MALE	0.9970
6	FEMALE	FEMALE	1.0000
7	FEMALE	FEMALE	1.0000
8	FEMALE	FEMALE	1.0000
9	FEMALE	FEMALE	1.0000
10	FEMALE	FEMALE	0.9999
11	FEMALE	FEMALE	1.0000
12	FEMALE	FEMALE	0.9966
13	FEMALE	FEMALE	1.0000
14	MALE	MALE	0.9524
15	MALE	MALE	1.0000
16	MALE	MALE	0.9627

Table 12. Replicated Goodness of Fit Test of the non-randomness of the sex ratio using study sites as replicates (Sokal and Rohlf, 1981).

SITE	MALES	FEMALES	TOTALS	G	p
ONE	29	13	42	6.18	< 0.025
TWO	30	45	75	3.00	> 0.1
THREE	10	4	14	2.57	> 0.1
FOUR	45	30	75	3.00	> 0.1
TOTALS	114	92	206		

H_1: Sites are homogenous for sex ratio.

G = 12.60 $p < 0.01$

reject H_1

H_2: The pooled sex ratio is 1:1.

G = 2.35 $p > 0.1$

accept H_2

H_3: The sex ratio in all sites is 1:1.

G = 14.95 $p < 0.005$

reject H_3

Table 13. Sex ratio as a function of time in site two. The ratio for each month was tested separately.

	MAY	JUNE	JULY	AUGUST	SEPTEMBER
MALES	12	11	10	8	2
FEMALES	11	18	18	27	7
G	0.04	1.68	2.28	10.74	2.79
p	> 0.1	> 0.1	> 0.1	< 0.005	> 0.1

Table 14. Sex ratio as a function of time in site four. The ratio for each month was tested separately.

	MAY	JUNE	JULY	AUGUST
MALES	8	10	7	1
FEMALES	7	10	8	8
G	0.65	0.00	0.65	5.87
p	> 0.1	> 0.9	> 0.1	< 0.025

Discussion

Population estimates

The first assumption of the Jolly-Seber method -- that census time is short -- was generally met. Censuses lasted a maximum of four hours within a site and the census interval ranged from two to ten days. However, catchability differed between females with known nest sites and those with no known nest (see Part Two). Moreover, catchability varied over the season resulting from greater difficulty capturing animals in warm weather and presumed changes in activity and habitat use over the summer. Heavy rain the night before also reduced the number of animals captured in a census, artificially lowering the estimate of population size. As a result of the effects of weather on both catchability and behaviour, it is difficult to separate mortality from changes in habitat or activity.

Fitch (1954) also reported reduced numbers of animals captured late in summer, particularly with respect to adult males. He suggested that a true estimate of sex ratio or age structure should be based on samples taken between the emergence from hibernation and onset of the breeding period. Fitch noted that because of the patchy distribution of animals and the seasonal variability, "no precise measurements of population density can be made". Excluding the rock pile where he found unusually high densities of animals, Fitch gave a range of 101 to 227 animals per ha.

These values are based on total captures within a year, excluding hatchlings. This compares with a range of 32 to 158 animals per hectare at Point Pelee.

Although Fitch reported a great deal of inter-year variation in the success of cohorts, in general he found that hatchlings more than doubled the population, yearlings made up 35 per cent of individuals (exclusive of hatchlings) and two-year olds made up 55 per cent of mature adults. In this study, hatchlings increased the population 114 per cent and yearlings made up 33 per cent of the population. The proportion of two-year olds could not be determined. Although there is a great deal of variability and uncertainty associated with these values the results suggest that the age structure of the population at Point Pelee is comparable to that studied in Kansas.

Growth Rate

The growth rate decreased gradually as animals increased in size, from a rate of 0.6 mm per day in hatchlings to zero in full grown adults. Fitch (1954) reported a maximum growth rate of 0.5 mm per day with an average of 0.35 mm per day among newborn hatchlings from the Kansas population. Therefore, there is no evidence to suggest that growth rates are slower in the Point Pelee population than in more southerly locations although of course further data would be needed to verify this. These data do seem to confirm that

animals in the Point Pelee population can reach sexual maturity in the same length of time as those in Kansas.

Reproductive Biology

Both Fitch (1954) and, Vitt and Cooper (1986) reported that age at sexual maturity was 21 months or the beginning of the second summer after hatching. However, Fitch reported the size at sexual maturity as being 60 mm svl whereas Vitt and Cooper reported seeing brooding (sensu Somma, 1988) females at 52 mm svl (Cooper, 1989, pers. comm.). The smallest reproductive female found at Point Pelee was first captured on August 3, brooding 8 eggs. She was 59 mm svl at that time but was presumably smaller at the time that she bred. The smallest male with breeding colours caught at Point Pelee was 52 mm svl on June 5. Another male that was 54 mm svl and had breeding colours on June 6 was only 47 mm svl on May 9. The smallest of six yearlings captured after August 1 was 57 mm svl so these males may not have been two-year olds and probably did not breed. Males and females may reach sexual maturity at different sizes.

Fitch (1954) suggested that in the more southerly populations some individuals may attain breeding size in their first summer, and that in more northerly populations some individuals may take three years. In contrast, it appears that some individuals at Point Pelee are able to attain minimum adult size by the beginning of their first summer although it is unlikely that such individuals would reproduce successfully until the following year.

In Kansas, breeding took place in late spring and one clutch of eggs was laid several weeks later. The exact timing of reproductive events varied yearly, occurring earlier in warm, dry years than in cool, wet years (Fitch, 1954). Comparison with data in Fitch (1954) suggests that the Point Pelee animals differ from Kansas populations in emerging from hibernation up to two weeks later. Breeding females retained their eggs for a substantially longer period of time (52 days versus 30-44 days in Kansas) but brooded them for a relatively short period (13 days versus 11-32 days in Kansas). This suggests that animals in the northern part of the distribution may make up for a shorter reproductive season by adjusting the length of time eggs are retained. Clutch size, at Point Pelee averaged 9.36 (n = 14) eggs which is similar to values reported elsewhere (Cagle, 1940; Fitch, 1954).

Clutch size in birds and lizards has been the subject of much discussion in ecology. Cody (1966) suggested that organisms face a tradeoff between clutch size (reproductive effort), competitive ability and predator avoidance. Williams (1966) proposed an inverse correlation between clutch size and lifespan.

Among lizards there appear to be two distinct strategies. Some lizards are small, short-lived, early maturing and iteroparous while others are relatively large, long-lived, late maturing and semelparous or annually breeding (Tinkle, 1969; Tinkle et al., 1970). The latter group tend to be temperate species and include all viviparous and brooding species including Eumeces fasciatus. In examining four populations of the lizard Sceloporus undulatus (Iguanidae), Tinkle and Ballinger (1972) found significant differences in clutch size, clutch frequency, body size and age at maturity which they associated with differences in growing season and predation risk. The differences were sufficiently great that different populations of the same species exhibited both distinct life history strategies. In view of these results, the apparent constancy in life history characteristics (clutch size, age at maturity) of the five-lined skink suggests that Kansas and Point Pelee may not present vastly different environments from the skink's point of view. Alternatively, there may be a lack of the genetic variability required for differences to evolve.

Several female skinks may lay their eggs under the same object or even in the same nest (Noble and Mason, 1933; Fitch, 1954). Female skinks apparently cannot distinguish their own eggs from those of conspecifics (Vitt and Cooper, 1986, 1989; Somma, 1989a) or even of congenerics (Vitt and Cooper, 1989) which could lead to one female brooding the eggs of another (E. fasciatus and E. laticeps, Noble and Mason, 1933; E. septentrionalis, Somma, 1987).

Females remain with the nest, apparently regulating moisture, turning the eggs regularly or moving the eggs in the case of flooding or high disturbance levels (Noble and Mason, 1933). Eggs which have rotted may be eaten to prevent contamination of the whole clutch (Somma, 1989a). Ingestion of live eggs may be a result of insufficient food or water (Vitt and Cooper, 1986). Hasegawa (1984) found that removal of females from nests of E. okadae increased egg mortality from an average of 8.5 per cent (n = 35) to an average of 95.9 per cent (n = 18).

Somma and Fawcett (1989) subjected clutches of E. septentrionalis eggs to three moisture regimes, with and without a brooding female. Egg mortality was minimized at a soil moisture of 15-20 per cent versus wetter or drier conditions. In all treatments, presence of the female improved survivorship. Brooding females responded to the treatment by increasing physical contact between the eggs and themselves, other eggs or the soil when the soil was too dry,

and by decreasing such contact when the soil was too wet. Females spent the greatest amount of time away from the nest when soil moisture was optimal. Soil moisture content was positively correlated with hatchling size (Somma, 1989b).

No quantitative measurements of soil moisture were made, but it was noted in this study that nests were usually tended by a female and that the soil near a nest appeared moister than that surrounding the nest area. Some authors have suggested that females will actually void water to moisten a nest (Fitch, 1954). I noted, especially after rain, that animals were certainly capable of voiding "water" when captured. Since these lizards excrete nitrogenous waste as uric acid, this "water" should not be construed as being urine.

Survivorship of hatchlings to adulthood likely varies with weather so the reproductive rate of the Pelee population cannot be determined at this moment. Fitch (1954) estimated that the average clutch recruited one individual into the breeding population by the time two years had passed, requiring that the average adult breed twice to replace itself.

Nest predation, either by small carnivores such as shrews, weasels, or raccoons, or possibly by vandals resulted in the loss of 4 of the 14 nests which were monitored at Point Pelee. A fifth nest was probably destroyed by a fungal infection and two additional nests suffered heavy losses to fungal attack. Sources of egg mortality in the study by

Hasegawa (1984) included soil invertebrates and cannibalism by large adults. The study was conducted on an island with no potential predators larger then adult E. okadae itself.

Sexual Dimorphism

Males were found to have significantly larger head widths and tail widths than females. Prior to oviposition, females were significantly heavier than males as a result of being gravid. After oviposition females weighed significantly less than males as a result of lipid resources used to develop and brood the eggs. There is some indication that males were longer than females after oviposition. However, growth rates did not differ significantly and therefore this may be a spurious result.

Eumeces fasciatus may be compared with the two related species, E. laticeps and E. inexpectatus in terms of sexual dimorphism. Vitt and Cooper (1985, 1986) found that E. laticeps and E. inexpectatus males were larger than females, but found no difference in E. fasciatus. In all three species, males had relatively larger heads than females and developed bright orange head colouration during the breeding period.

Testosterone implants induce breeding colouration and aggressive behaviour in E. laticeps (Cooper et al., 1987). Males of the three species recognize conspecifics from olfactory cues and direct aggression toward conspecific males

exclusively (Cooper and Vitt, 1987b,c). Artificially colouring the heads of female E. laticeps induced agonistic behaviours in male conspecifics but olfactory signals proved a stronger counteracting cue (Cooper and Vitt, 1988). Small males tended to avoid agonistic encounters with large males (Cooper and Vitt, 1987a). Large males were more likely to be seen guarding mates (Vitt and Cooper, 1985b). In contrast, no physical differences were found between males found with and without females in this study.

The relationship between testosterone and breeding colours suggests that males without breeding colours would not be capable of breeding. None of the males that I identified by the discriminant function analyses were captured during the height of the breeding period. All males captured during the breeding period had breeding colours. Thus it appears unlikely that a sneaker strategy (Kodric-Brown, 1986) could or has evolved in this species. I also found no relationship between physical attributes and whether a male was found with a female during the breeding period. Yearlings with faint male breeding colours were occasionally captured with adult males, but showy adult males were never captured together. However, adult males were occasionally seen basking together at the same microsites although on one such occasion this led to a chase.

Sexual dimorphism has been attributed to two possible causes. First, sexual selection acting on only one sex may

cause the sexes to differentiate. Second, differences between the sexes may facilitate resource partitioning and therefore could arise from selection to reduce intra-sexual competition. To test the hypothesis that head width dimorphism in E. laticeps was a result of selection for niche differentiation, Vitt and Cooper (1985) examined stomach contents of males and females. Prey size was correlated with body size and head size and males tended to eat larger prey than females. Nevertheless, both sexes were known to consume much larger prey than were found. Vitt and Cooper (1985) suggest that resource partitioning is a result and not a cause of sexual dimorphism.

Fitch (1981) examined sexual size differences in reptiles and found that of the 770 taxa for which data existed, 371 had females averaging larger than males, 374 had males averaging larger than females and 25 had males and females approximately the same size. Wide-ranging species, such as Uta stansburiana (Iguanidae) and Cnemidophorus tigris (Teiidae), showed geographic variation for the degree and direction of sexual size dimorphism. Fitch (1981) suggested that the degree of sexual size dimorphism depends in part on the relation between size and fecundity in females and the degree to which fighting among males is associated with greater risk of predation or greater access to mates. However, no synthesis has been made of data on sex differences in the size of body parts independent of overall

size, in reptiles.

In many cases the traits affecting breeding success of males are strongly influenced by environmental conditions or age (Clutton-Brock, 1983; Kodric-Brown and Brown, 1984) and selection on a particular phenotypic trait may select for overall genetic superiority rather than for particular genes. In herptiles, size is often more strongly correlated with juvenile growth rate than with age (Halliday and Verrell, 1988) and this in turn may be influenced by egg size or amount of yolk, date of hatching or early environment. Trivers (1976) found that large male Anolis garmani (Iguanidae) defended larger territories and copulated more frequently than small males. He also found that large males had higher growth rates as juveniles but were not necessarily older. In Urosaurus ornatus (Iguanidae), polygynous males are significantly larger than monogamous males but the frequency of polygyny is habitat dependent (M'Closkey, et al., 1990a).

Sexual dimorphism may have several causes acting concurrently on a given species. Therefore, experimental studies are needed to disentangle the relative roles of habitat, resource distribution, access to mates and parental effort.

Sex Ratios

If parental investment in male and female offspring is equal then one expects the intrinsic (i.e. primary) sex ratio in a population to be 0.5 (i.e. 1:1) (Fisher, 1958). In organisms where sex is chromosomally determined a 1:1 sex ratio is easily achieved in the products of meiosis and no additional mechanisms are required. Wright (1973) first reported chromosomal sex determination in a Scincid lizard, Scincella laterale, but noted that no such sex differences were found in several species of the genus Eumeces (Deweese and Wright, 1970).

However, in examining mating systems it is not the intrinsic sex ratio which is important but rather the operational sex ratio (OSR) or the ratio of sexually receptive females to sexually active males during the breeding period. Only site one out of the four sites studied had a significantly biased sex ratio although in all four sites there were more males than females captured during the month of May (the breeding period). Trivers (1972) indicated that unless the sex ratio is highly skewed it may take very large numbers of animals to give a significant result. Fitch (1954) reported a highly male biased sex ratio (100:122.6) but did not discuss how he determined sex.

Given the differences in sex ratio I observed between site one and the other sites, there may be local, habitat dependent variation in the potential for polygamy. This may

provide an opportunity to examine the role of habitat in the mating system of the five-lined skink.

Although the sex ratio was not in general significantly biased during the mating period at Point Pelee, the sex ratio became female biased later in the summer at both sites two and four. This resulted from a combination of two factors. The number of females captured increased because females who had nested inside logs emerged from them. Simultaneously, the number of males captured decreased. This decrease in male activity was also noticed by Fitch (1954) who suggested that they may retreat underground to escape the heat of late summer.

Conclusion

Cooper and Vitt (1988) suggested that the breeding colouration of male E. laticeps evolved through sexual selection. They based their conclusion on the observation that breeding males reacted aggressively to the sight of such breeding colours. However, this is not sufficient evidence for the action of sexual selection. Ultimately, it is necessary to show that variation in breeding colouration is heritable and that it influences reproductive success under natural conditions.

Because Eumeces spp. are also sexually dimorphic for head width and breeding colouration is displayed on the head, it is plausible to suggest that there is a functional link between the two character traits. The observation that male head width in E. laticeps increases during the breeding period is consistent with this hypothesis (Vitt and Cooper, 1985). Unfortunately, there were insufficient recaptures of adult males, in the present study, to test whether this increase is also true of E. fasciatus. An alternative hypothesis, rejected by Vitt and Cooper (1985) for E. laticeps, is that head width dimorphism is associated with evolution to reduce competition for food between the sexes.

What opportunities exist for sexual selection to operate in the five-lined skink? The sex ratio at Point Pelee appears to be unbiased. Males captured with females did not significantly differ in svl, head width, or tail width from

males not captured with females. In part two I shall present evidence that E. fasciatus is not territorial. Nonetheless, males do fight during the breeding period (Fitch, 1954; pers. obs.) and females do invest significantly greater effort in parental care than do males.

Further clarification of the processes involved in the evolution of sexual dimorphism in the Fasciatus group may result from comparative studies. Eumeces laticeps appears to exhibit a more advanced degree of dimorphism -- greater differences in head width, differences in svl. This species also may be territorial (Stamps, 1977). Eumeces inexpectatus is also dimorphic in svl. Is it territorial? What are the mechanisms of mate selection in these species? These are difficult questions to answer but their answers will provide insight into how sexual selection works.

PART TWO

SPATIAL DISTRIBUTION AND MICROHABITAT USE OF *EUMECES FASCIATUS* AT POINT PELEE NATIONAL PARK

Introduction

Patterns in spacing behaviour among animals are generally described using two concepts: home range and territory (Waser and Wiley, 1979). Home range commonly refers to the area in which an animal spends the majority of its time. Any part of that area which an animal defends against intruders is called a territory (Noble, 1939). Stamps (1977) suggested that territoriality generally falls into one of three categories: home range defence, specific site defence, and non-territorial behaviour. Further gradients in these behaviours can be defined with reference to the relationship between an animal's activity, isolation, and probability of attack or retreat as a function of location (Waser and Wiley, 1979).

The order Squamata includes two divisions of lizards, Ascalabota and Autarchoglassa (Camp, 1923). Most members of the Ascalabota (including iguanids) defend territories or specific sites and are visually orientated sit-and-wait foragers (Stamps, 1977). Members of the Autarchoglassa (including skinks) differ in relying both on olfaction and

vision to locate prey and in actively searching for prey (Camp, 1923). Few Autarchoglassa defend territories although some do defend specific sites.

Poor visibility, resulting from the foraging mode in skinks, is cited as inhibiting detection of intruders (Fitch, 1954; Stamps, 1977). Thus, territorial defence may not be economically feasible in skinks (Brown, 1964). Defence of specific sites, such as shelters, basking sites, or nest cavities appears to be unaffected by poor visibility, but is affected by the frequency of use (Stamps, 1977). Skinks would have little opportunity to defend a territory but may defend shelter sites (Bustard, 1970), basking sites (Whitaker, 1968), or exhibit exclusive occupancy without defence (Breckenridge, 1943; Fitch, 1955).

Territorial species may exhibit a clumped distribution as a result of conspecific cuing (Stamps, 1988a). However, the pattern of aggregation is only apparent with respect to the total habitat available. Within occupied habitats, territorial species tend to have a uniform distribution. Therefore, a clumped distribution with respect to occupied microsites would provide evidence that the five-lined skink does indeed lack territoriality.

Habitat and Microhabitat

A great deal of research in ecology over the last thirty years has focused on the concept of the ecological niche. Hutchinson (1957) defined the fundamental niche of a species as a hypervolume in a multidimensional space of environmental variables describing the states of the environment over which a species could survive indefinitely. The realized niche of a species was defined as that subset of the hypervolume corresponding to the states of the environment in which the species was actually found. The realized niche may differ from the fundamental niche as a result of historical factors or biological interactions such as predation and competition. In practice, niches are usually defined in terms of habitat, food resources and time of activity (Cody, 1966; Pianka, 1975).

Habitat use by a population is a reflection both of decisions made by individual foragers as well as the effects of other species in the community. From the point of view of an individual forager habitats may be fine-grained (homogenous) or coarse-grained (patchy). The graininess of the habitat influences the foraging mode that an individual should adopt.

In fine-grained environments spatial variations are small relative to the mobility and perceptual ability of the forager. MacArthur and Pianka (1966) proposed that in such habitat the optimal forager will minimize the sum of the

pursuit and search costs through its choice of diet. The realized diet of the forager may then expand or contract without altering the realized habitat (Krebs et al., 1977).

In coarse-grained environments patches may differ in quality and the forager faces a trade-off between travel time to a patch and hunting time within a patch which is a function of the number of patch types used (MacArthur and Pianka, 1966). Within a patch, the marginal value theorem (Charnov, 1976) specifies when the forager should give up and move on to a new patch in order to maximize its energy intake. Giving up time (GUT) is a function of the change in rate of food intake as the animal depletes the resources available in the patch. The degree of resource patchiness in a habitat will also influence the potential for polygamy (Emlen and Oring, 1977).

Energy maximization, considered alone, ignores other factors which influence individual behaviour. For example, the presence of a potential predator may constrain the ability of an organism to maximize energy intake in favour of optimizing survival (Milinski and Heller, 1978; Sih, 1982). Choice of habitat will then influence predation risk (Werner, 1986) and age classes within a species may segregate between habitats because of differences in predation risk (Werner et al., 1983) or to avoid cannibalism (Sih, 1982). Habitat selection can also influence the mating system in a

population (M'Closkey et al., 1990b).

What are the proximate determinants of settlement patterns of individuals in populations? Individuals may use resources as cues in selecting a habitat, by responding to food abundance or habitat structure. In contrast, Kiester and Slatkin (1974) proposed that individuals could gain additional information about the distribution of resources by monitoring the activities of conspecifics. Juvenile Anolis aeneus (Iguanidae) prefer territories that have been previously occupied (Stamps, 1987). This preference was particularly true of younger, less experienced individuals (Stamps, 1988b). This process can lead to spatial aggregation (Stamps, 1988a).

Habitat selection by individuals may also be influenced by the prior choices of other members of the population. Fretwell and Lucus (1970) developed a model to predict when individuals should disperse from a high quality habitat to a low quality habitat. The model was based on the idea that fitness within a habitat was density dependent. Whitham (1980) found the model a good predictor of habitat selection by ovipositing female aphids (Pemphigus). The Fretwell-Lucus model was extended by Rosenzweig (1981) to include the case of two species competing in an environment with two patch types. In the case where competition between the species is by interference, the competitively subordinate species becomes less selective as the density of dominants increases.

At sufficiently high densities of the dominant, the subordinate may completely abandon the preferred habitat (Pimm et al., 1985). A further development of the model (Rosenzweig, 1989) proposed that two species may share a preferred habitat without competitive exclusion because at high densities they disperse to different habitats.

Density of conspecifics in a habitat may influence population level phenomena such as birth and death rates. However, Strong (1986) cautioned that because of the stochastic nature of the relationship between density and population growth, density dependent effects may be weak at intermediate population sizes and only become apparent at extremes. The distribution of conspecifics in a habitat also influences the degree of competition for mates (Davies and Lundburg, 1984) and the potential to monopolize mates (Emlen and Oring, 1977; M'Closkey et al., 1990b).

Habitat and Community Structure

Preferences along the habitat dimension of the niche may influence interactions between species along other dimensions (such as food) and thereby influence the structure of communities. Species packing models have been developed to try to determine the limits to niche overlap within a stable guild of species in a community (MacArthur and Levins, 1967; May and MacArthur, 1972; May, 1974). Such theories have been used to predict patterns of diversity an. species

composition. For example, May and MacArthur (1972) suggested that niche overlap is reduced in highly fluctuating environments but approaches a constant value under moderate variability.

Tests of these models led to examination of niche overlap in the field. Cody (1968) found that grassland bird communities segregated by habitat preferences and feeding behaviour. Vegetation height was a good predictor of the number of species and average niche overlap. Brown's (1975) studies of desert rodents have shown non-random patterns of habitat segregation. Pianka (1975) found that lizard communities on different continents differed in niche overlap, especially microhabitat use. M'Closkey (1978) showed that desert rodent communities were assembled so as to minimize niche overlap and therefore maximize resource use on axes of structural habitat.

More recent research has attempted to relate community organization to the economics of resource use by individual foragers in different patches of habitats (Brown, 1989; Kotler and Brown, 1988). Qualitative differences between patches as well as temporal and spatial variation will influence different species in different ways. Thus, coexistence of species may result from variable predation risk (Kotler, 1984), differences in foraging efficiency (Werner and Hall, 1977, 1979), and microhabitat selection (M'Closkey, 1978, 1985; Kotler and Brown, 1988). Seasonal

rotation in foraging efficiency (Brown, 1989) or repeated disturbances which prevent equilibration (Levins, 1979; Paine and Levin, 1981) may also promote coexistence.

Thus, examination of the habitat dimension of the niche has inspired significant theoretical and empirical research in behavioural (Krebs and Davies, 1981), population (Huey et al., 1983), and community (Cody and Diamond, 1975; Strong et al., 1984; Diamond and Case, 1986) ecology.

Goals of This Study

I examined patterns of microhabitat use in the five-lined skink with regards to several questions. Very little is known of the skink's microhabitat preferences. Therefore, my first goal was to determine which characteristics of habitats influence skink distribution and abundance. In addition I asked, whether this skink is territorial? What habitat is available to the skink at Point Pelee? How do park policies influence the distribution and abundance of skinks? And finally, is the skink an indicator of habitat succession or disturbance?

In this study, I test the hypothesis that the five-lined skink is not territorial by examining the spatial distribution of animals within a population of Eumeces fasciatus at Point Pelee National Park, Canada, in terms of aggregation and association among individuals. Males, females, yearlings and hatchlings are compared for number of

captures, catchability, residence time, site tenacity, and distance moved. Microhabitat preferences are examined by relating numbers of animals found at a location to physical (surface area, thickness, per cent shading and distance to nearest neighbour) and biological (presence of other skinks or nests) parameters.

My goal is to provide a quantitative description of microhabitat use and spatial distribution with the view to assessing the utility of the five-lined skink as a model organism in ecological studies.

Methods

Unless otherwise indicated, the data discussed in this section were collected in study sites two and four as described in Part One. I examined spatial distribution of animals within and among age and sex classes. The frequency distribution of the number of animals captured at each microsite, revealed the degree to which skinks, within an age or sex class, aggregate spatially. A chi-square test of the index of dispersion (I = variance/mean) compared this distribution to a Poisson (Krebs, 1989). The degree to which skinks in different age or sex classes associate was determined by examining whether the occurrence of one class of animal was independent of the occurrence of the other classes, at a microsite using a log-linear model (Sokal and Rohlf, 1981).

Data were divided into four time slots for this analysis. Male, female and yearling distributions were examined during the breeding period (May 16 - June 12), while females were gravid (June 13 - July 11) and while females were brooding (July 12 - August 1); hatchling distributions were examined from August 2 through the end of the season. Numbers of adults and yearlings were insufficient for tests after August 1. Separate analyses were conducted on sites two and four. An additional comparison was done in site two using groups of boards rather than single boards as the unit of measure. There were insufficient groups of boards in site

four to make this worthwhile. Hatchlings were not included in the analysis of association.

A resident (M'Closkey et al., 1987)is usually operationally defined as an animal captured two or more times within a study site. Because of the low catchability of the skinks not all animals captured only once are non-resident. I tested the assumption that all animals within the site were indeed residents by comparing the frequency of captures to a binomial distribution. If p is the probability of an animal being captured during a census then the frequency distribution of the number of animals caught r times in n censuses should approximate the binomial (p,n,r). Because I did not know the number of animals with zero captures, a zero truncated binomial (Johnson and Kotz, 1971) was employed (Appendix B). The ratio of the expected number of residents to non-residents was compared to the actual values using a G statistic (Sokal and Rohlf, 1981) and taking each study site, age, and sex class separately.

Tests of the independence of the ratio of residents to non-residents from age, sex, and site of capture were also conducted using a G statistic (Sokal and Rohlf, 1981).

Home range size was estimated as the minimum linear span (mls) of activity for an individual. This was calculated as the shortest line connecting all points of capture. Values that reached an asymptote as the number of captures increased were accepted as estimates of home range size. Otherwise

these values were interpreted as an estimate of mobility over a given time span.

Residence time (M'Closkey et al., 1987) was defined as the number of days between the first and last capture of each animal captured more than once. Catchability was defined as the ratio of the number of captures to the number of censuses conducted during the residency of the animal. Because catchability is a ratio, to achieve a normal distribution, it was arcsine transformed. Means and standard errors were re-transformed back to original units.

Analyses of variance (anova) were used to determine whether site of capture, time of capture, age or sex influenced the number of captures, catchability, residence time or number of microsites at which each animal was found. Homogeneity of variances was tested using the F_{max} test. When variances were heterogenous the non-parametric Kruskal-Wallis test was used. Within each site the effect of age and sex on capture statistics was also examined using a multivariate analysis of variance (manova).

Data from site two on number of captures and catchability was examined during three different time periods The period before oviposition was defined as starting at the beginning of the field season (April 28) and ending on July 11. The nesting and post-hatching periods were as defined above.

Five variables were used to characterize the microsites where animals were found: class of material, surface area, thickness of the cover, per cent shading and distance to nearest neighbour. Six classes were used to define the material. Class one consisted of scattered small pieces of wood including bits of drift wood. Class two microsites were solid or hollow logs. Thin planks, made up class three. Boards, class four, were defined as thin pieces having nearly equal length and width. Class five consisted of thick beams such as the cross-bars from telephone poles. Finally, class six objects were rotted logs. Only two animals were ever found under non-woody debris. One was found under sandbag cloth in site one: One was found under a strip of hard plastic in site two.

Per cent shading was determined by the degree to which the microsite was surrounded by shading vegetation. A microsite that was under the overhanging branches of a tree was considered one hundred per cent shaded, while one in the middle of a meadow with no bushes nearby was considered zero percent shaded. Values of shading were selected from the following set: 0, 10, 25, 50, 75, 90, and 100.

Average-linkage cluster analysis was used to group microsites on the basis of surface area, thickness of the cover, shade, and distance to nearest neighbour. Clusters were compared for the total number of animals found at the microsites as well as the number of males, females,

yearlings, and hatchlings.

Changes in microhabitat preferences over the season were examined by looking at numbers of animals of different classes found during different time periods. The four time periods used in spatial analysis (above) were also used here.

There are three sources of the woody debris under which skinks were found. Most debris washes up onto the beach from Lake Erie and is gradually incorporated into the advancing line of vegetation. This may consist of anything from large drift logs and the gunwales of shipwrecked boats to small bits of flotsam. Some debris is directly derived from the vegetation on the dunes and consists of fallen branches or tree trunks. Finally, boards, beams and planks may be left behind by maintenance staff.

Each piece of debris, or in some cases each pile of pieces, was designated a microsite and its location was mapped. Microsites could be distinguished as being of natural or artificial origin. A manova was used to determine whether natural and artificial microsites differed physically. Analysis of covariance was used to determine whether they differed for the number and type of animals found. In all cases, parametric tests were only performed when variances were homogenous by Bartlett's Fmax test (Sokal and Rohlf, 1981). Otherwise non-parametric methods were used.

Results

Spatial Distribution

Of the thirteen chi-square tests of spatial aggregation done on site two data, seven demonstrated significant aggregation of like animals (Table 15). Using groups of boards increased this to nine significant results out of thirteen (Table 16). At site four, there was only sufficient data to conduct seven of the thirteen tests. Three were significant (Table 17).

The association between animals of different ages or sexes was examined by determining the number of boards under which different combinations of animals occurred. At site two (Table 18) the interaction among males, females, and yearlings (MFY) was insignificant at all times. During the breeding period there was a significant interaction between the presence of males and females under boards independent of the presence of yearlings (MF(Y)). Therefore, the hypothesis of independence of male, female and yearling location (M F Y) during the breeding period was rejected. Significant interaction among location of males, females, and yearlings, at site four (Table 19) during the breeding period meant the interaction between males and females had to be tested separately with and without yearlings. Only in the presence of yearlings (MF(Y=P)), was there a significant interaction between males and females. While females were gravid, this interaction was independent of yearlings.

Table 15. Chi-square analysis of the aggregation of like animals at 56 microsites at site two. I is the index of dispersion.

SEASON		ALL	MALES	FEMALES	YEARLINGS	HATCHLINGS
BREEDING	I	1.699	1.618	1.153	1.055	-----
	x^2	93.45	89.00	63.40	58.00	-----
	p	<0.001	<0.005	n.s.	n.s.	-----
GRAVID	I	3.305	1.127	2.348	1.696	-----
	x^2	181.78	62.00	129.15	93.27	-----
	p	<0.001	n.s.	<0.001	<0.001	-----
NESTING	I	1.544	.891	1.309	1.248	-----
	x^2	84.93	49.00	72.00	68.67	-----
	p	<0.01	n.s.	n.s.	n.s.	-----
HATCHING	I	-----	-----	-----	-----	5.655
	x^2	-----	-----	-----	-----	311.0
	p	-----	-----	-----	-----	<<0.001

Table 16. Chi-square analysis of the aggregation of like animals at 39 groups of microsites at site two. I is the index of dispersion.

SEASON		ALL	MALES	FEMALES	YEARLINGS	HATCHLINGS
BREEDING	I	3.207	2.530	2.269	0.951	-----
	X^2	121.87	96.12	86.24	36.14	-----
	p	<0.001	<0.001	<0.001	n.s.	-----
GRAVID	I	3.785	1.072	2.263	2.274	-----
	X^2	143.83	40.75	86.00	86.40	-----
	p	<0.001	n.s.	<0.001	<0.001	-----
NESTING	I	2.103	1.135	1.908	1.211	-----
	X^2	79.93	43.13	72.50	46.00	-----
	p	<0.001	n.s.	<0.001	n.s.	-----
HATCHING	I	-----	-----	-----	-----	6.283
	X^2	-----	-----	-----	-----	238.7
	p	-----	-----	-----	-----	<<0.001

Table 17. Chi-square analysis of the aggregation of like animals at 28 microsites in site four. I is the index of dispersion.

PERIOD		ALL	MALES	FEMALES	YEARLINGS
BREEDING	I	1.302	----	----	2.095
	X^2	36.46	----	----	58.67
	p	n.s.	----	----	<0.001
GRAVID	I	1.663	0.831	0.831	2.202
	X^2	46.57	23.27	23.27	61.67
	p	<0.025	n.s.	n.s.	<0.001
NESTING	I	0.853	----	----	----
	X^2	23.89	----	----	----
	p	n.s.	----	----	----

Table 18. Log-linear analysis of the interaction among males, females, and yearlings for location of capture at site two.

SEASON INTERACTION		MFY	MF(Y)	MY(F)	FY(M)	M F Y
BREEDING	G	1.021	7.755	1.221	0.241	12.175
	d.f.	1	1	1	1	4
	p	n.s.	<0.049	n.s.	n.s.	<0.049
GRAVID	G	0.002	3.004	6.768	0.519	10.778
	d.f.	1	1	1	1	4
	p	n.s.	n.s.	n.s.	n.s.	n.s.
NESTING	G	1.983	7.132	0.231	0.051	9.529
	d.f.	1	1	1	1	4
	p	n.s.	n.s.	n.s.	n.s.	n.s.

Table 19. Log-linear analysis of the interaction among males, females, and yearlings for location of capture at site four.

SEASON	INTERACTION	MFY	MF(Y=A)	MF(Y=P)
BREEDING	G	4.963	0.035	5.044
	d.f.	1	1	1
	p	<0.05	n.s.	<0.025

	INTERACTION	MFY	MF(Y)	MY(F)	FY(M)	M F Y
GRAVID	G	1.349	6.907	0.451	0.451	11.140
	d.f.	1	1	1	1	4
	p	n.s.	<0.02	n.s.	n.s.	n.s.

Residence and Movement

The assumption that all animals within the site were residents was tested by comparing the frequency of captures to a zero truncated binomial distribution (Johnson and Kotz, 1971, Appendix B). The ratio of the expected number of residents to non-residents was compared to the actual values using a G statistic (Sokal and Rohlf, 1981) and taking each study site and each segment of the population separately (Table 20). Only in site four was the number of non-resident females significant. In site one, the number of non-resident males was significant. The number of non-resident yearlings was significant in all sites except site one.

The interactions between the ratio of residents to non-residents and age, sex and site of capture were tested by a G test (Table 21). Sex was found to interact significantly with the residence ratio such that females were more likely to be resident than males. The other interactions were not significant.

For animals that were captured more than once, I examined whether they were always captured at the same location and the distance between locations where they were found. The minimum linear span (mls) of activity for each resident animal was calculated. If the minimum linear span reached an asymptotic value with respect to the number of captures, it was considered to be a true representation of the range of the animal. Data were examined for 88 animals

Table 20. G-Test of the ratio of residents to non-residents compared to that predicted by a zero truncated binomial.

	MALES	FEMALES	YEARLINGS	ALL
SITE ONE				
EXPECTED	10.4:18.6	4.7:8.3	6.8:12.2	
OBSERVED	4:25	3:9	10:9	
G	7.014	0.624	2.164	10.006
p	< 0.01	> 0.10	> 0.05	< 0.025
SITE TWO				
EXPECTED	18.7:8.3	29.7:13.3	18.7:8.3	
OBSERVED	14:13	29:14	10:17	
G	3.431	0.055	11.522	15.286
p	> 0.05	> 0.10	< 0.001	< 0.005
SITE THREE				
EXPECTED	4.6:5.4	2.3:2.7	6.6:8.1	
OBSERVED	3:7	2:3	3:12	
G	0.977	0.059	4.192	5.423
p	> 0.10	> 0.10	< 0.05	< 0.05
SITE FOUR				
EXPECTED	13.2:1.8	13.3:1.7	12.3:1.7	
OBSERVED	11:4	9:5	6:8	
G	2.316	5.097	15.819	24.056
p	> 0.10	< 0.025	< 0.001	< 0.001

Table 21. G-Test of the interactions between residence ratio and age, sex and site of capture.

	RESIDENT	NON-RESIDENT	G	p
AGE x RESIDENCY				
ADULT	81	131	3.16	> 0.05
YEARLING	28	72		
SEX x RESIDENCY				
MALES	35	81	6.96	< 0.01
FEMALES	46	50		
SITE x RESIDENCY				
SITE ONE	19	45	5.91	> 0.05
SITE TWO	55	72		
SITE THREE	8	22		
SITE FOUR	33	71		

of whom 33 displayed a null range of activity and 29 did not reach asymptotic values. If the asymptote is only accepted after it remained constant for three or more captures then the number of acceptable non-zero values drops to eight. Of these eight values there were five adult females, one adult male, one yearling male, and one yearling of unknown sex. Therefore, no test of significance could be made.

The data for all animals in sites two (Figure 8) and four (Figure 9) are displayed in a frequency histogram, but should not be interpreted as representing home range sizes, but merely as giving some indication of the degree to which animals moved large or small distances. The values represent the minimal distance travelled that includes all points of capture. A hatchling moved the longest distance, 107.5 metres. A second hatchling travelled 68.7 metres. The longest movement by a yearling was 25 metres. Two females moved 68 metres. One of these moved this distance prior to the time of oviposition and returned to the original location of capture shortly after the time of hatching. Two other females made similarly timed movements away from the first point of capture and later returned to or near to that point. These females moved 23 and 37 metres. The longest movement by a male was 52 metres.

Figure 8. Minimum linear span of males (solid), females (hatched), yearlings (stippled) and hatchlings (open) at site two.

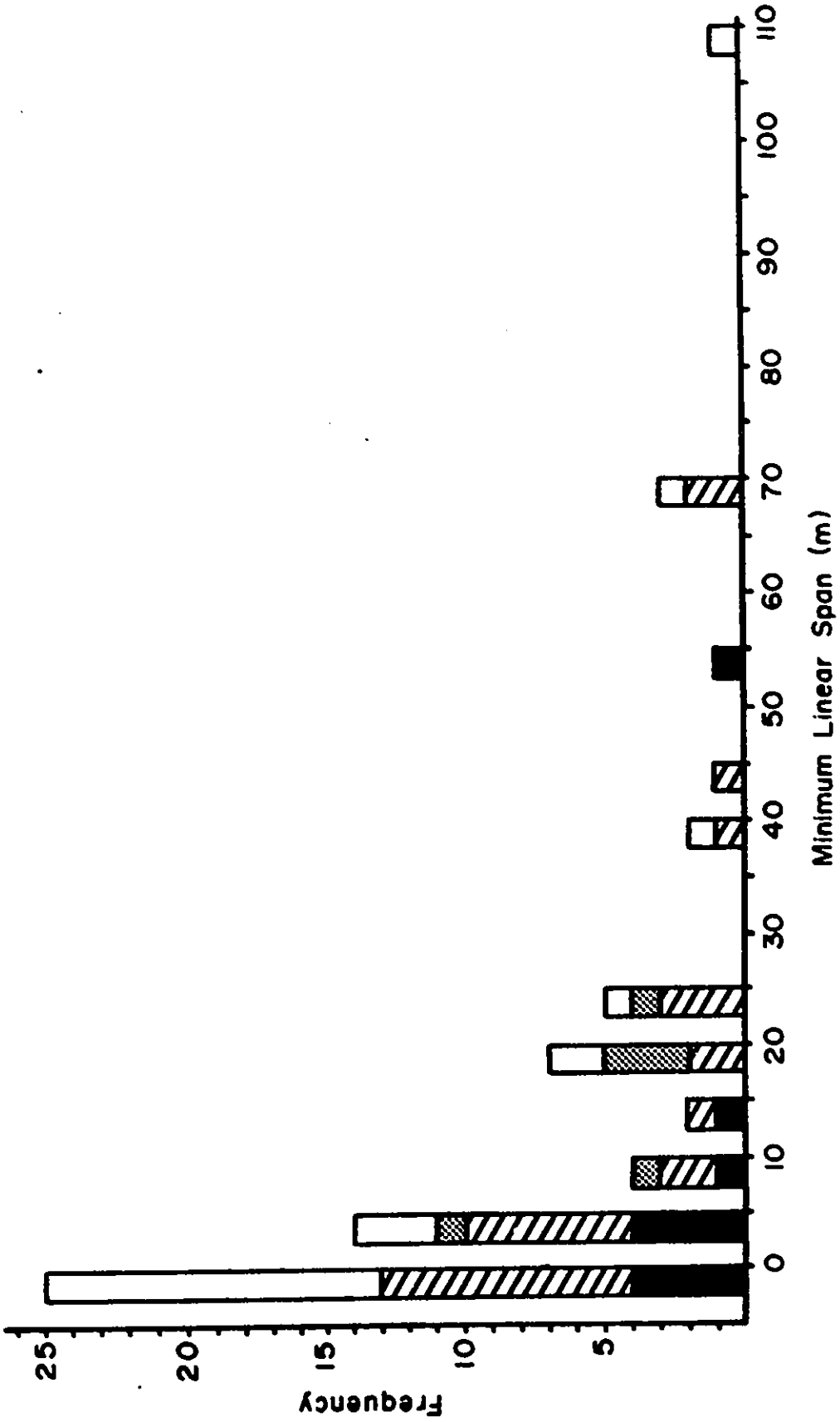
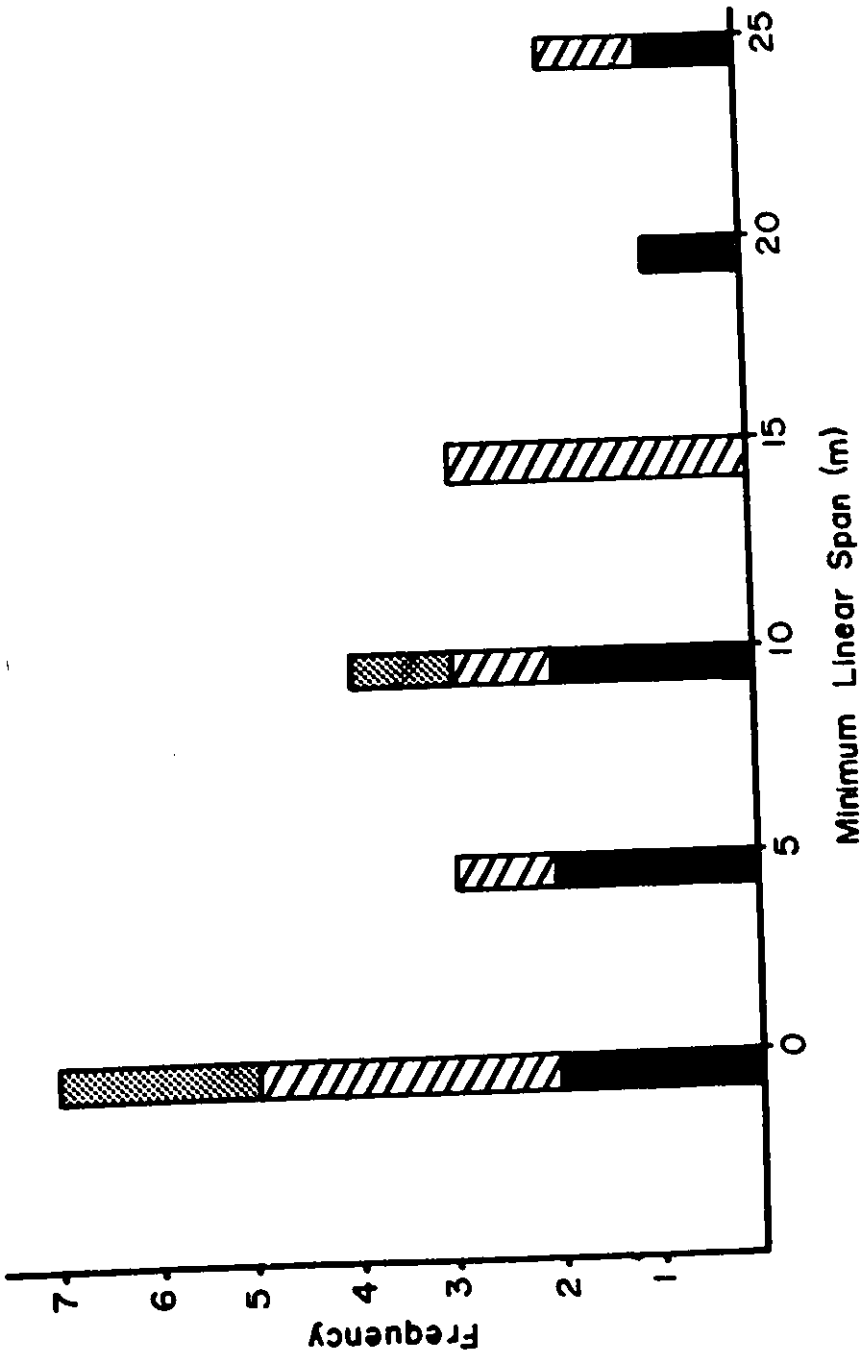

Frequency
25
20
15
10
5
0
10
20
30
40
50
60
70
80
90
100
110
Minimum Linear Span (m)

Figure 9. Minimum linear span of males (solid), females (hatched) and yearlings (stippled) at site four.


Minimum Linear Span (m)
0
5
10
15
20
25
Frequency
1
2
3
4
5
6
7

When sex and age classes of the population were compared using the Kruskal-Wallis test no significant difference was found for rank scores ($X^2 = 3.37$, $p = 0.5$). Distance moved was weakly correlated with the number of times an animal was caught ($r = 0.26$, $p < 0.05$).

Capture Statistics

Four variables were derived to describe the capture characteristics of each animal: number of captures, residence time, catchability, and number of microsites inhabited. Study sites differed for residence times and catchabilities but not for the number of captures or the number of microsites occupied by each animal (Table 22) because of small sample sizes in sites one and three all subsequent analyses were conducted on data from sites two and four. Yearlings occupied more microsites than adults at site two (Table 23). There were no differences at site four (Table 24). Male and female adults were compared and no significant differences were found at either site (Tables 25 and 26).

Number of captures and catchability were recalculated over three distinct time periods. In addition, females were divided into those whose nest site was known and those with no known nest site. Only site two data had sufficient sample sizes for this analysis. Prior to oviposition, there was no difference among the groups. After oviposition females with

Table 22. Analyses of variance comparing study sites. Non-parametric tests were conducted when variances were heterogeneous. Catchability was arcsine transformed but means and variances are reported for back-transformed data. Means with different superscript letters differ significantly (Scheffe's multiple comparison, $p < 0.05$).

SITE		NUMBER OF CAPTURES	RESIDENCE TIME	CATCH-ABILITY	NUMBER OF MICROSITES
ONE	$\overline{X}$	2.47 a	22.0	0.9676 a	1.93 a
	SE	0.14	2.4	0.0053	0.18
TWO	$\overline{X}$	3.27 a	47.5	0.5410 b	1.96 a
	SE	0.21	4.7	0.0020	0.11
THREE	$\overline{X}$	3.25 a	22.75	0.9250 ac	1.25 a
	SE	0.27	5.36	0.0147	0.16
FOUR	$\overline{X}$	3.15 a	34.79	0.7790 c	1.63 a
	SE	0.27	4.39	0.0047	0.11
x^2		1.52	4.88	----	----
F		----	----	14.64	3.2
p		0.299	0.015	0.0001	0.262

Table 23. Analyses of variance comparing age classes for capture statistics at site two. catchability was arcsine transformed but means and variances are reported for back-transformed data.

		NUMBER OF CAPTURES	RESIDENCE TIME	CATCH-ABILITY	NUMBER OF MICROSITES
ADULTS	$\overline{X}$	3.18	46.18	0.5653	1.82
	SE	0.24	5.37	0.0029	0.11
YEARLINGS	$\overline{X}$	3.89	60.22	0.4361	2.67
	SE	0.45	9.47	0.0036	0.24
ANOVA	F	2.61	1.31	1.21	8.95
	p	0.11	0.26	0.28	0.004
MANOVA	F = 2.48		p = 0.056		

Table 24. Analyses of variance comparing age classes for capture statistics at site four. Catchability was arcsine transformed but means and variances are reported for back-transformed data.

		NUMBER OF CAPTURES	RESIDENCE TIME	CATCH-ABILITY	NUMBER OF MICROSITES
ADULTS	$\bar{X}$	3.33	38.15	0.7746	1.67
	SE	0.31	4.94	0.0058	0.12
YEARLINGS	$\bar{X}$	2.40	23.20	0.7175	1.60
	SE	0.40	7.62	0.0311	0.4
ANOVA	F	1.55	1.55	0.12	0.04
	p	0.22	0.22	0.74	0.84
MANOVA	F = 1.11		p = 0.37		

Table 25. Analyses of variance comparing adult males and females for capture statistics at site two. Catchability was arcsine transformed but means and variances are reported for back-transformed data.

		NUMBER OF CAPTURES	RESIDENCE TIME	CATCH-ABILITY	NUMBER OF MICROSITES
MALES	$\bar{X}$	2.71	43.71	0.6184	1.64
	SE	0.30	9.62	0.0149	0.17
FEMALES	$\bar{X}$	3.39	48.46	0.5057	1.89
	SE	0.33	7.14	0.0028	0.15
ANOVA	F	1.73	0.15	1.00	1.07
	p	0.19	0.70	0.32	0.31

MANOVA F = 1.33 p = 0.28

Table 26. Analyses of variance comparing adult males and females for capture statistics at site four. Catchability was arcsine transformed but means and variances are reported for the back-transformed values.

		NUMBER OF CAPTURES	RESIDENCE TIME	CATCH-ABILITY	NUMBER OF MICROSITES
MALES	$\bar{X}$	3.07	31.50	0.8506	1.57
	SE	0.37	5.88	0.0105	0.17
FEMALES	$\bar{X}$	3.67	47.25	0.6338	1.75
	SE	0.56	8.23	0.0113	0.18
ANOVA	F	0.84	2.53	2.91	0.51
	p	0.37	0.12	0.10	0.48
MANOVA	F = 0.75		p = 0.57		

known nest sites had a significantly higher capture rate than the other groups. After hatching, these females and the yearlings had a lower capture rate (Figure 10). A Kruskal-Wallis test was required to compare catchability prior to oviposition therefore differences among groups could not be determined. While nesting, catchability was significantly higher in females with known nest sites versus those with unknown nest sites. After hatching, the pattern was reversed but the differences were not significant (Figure 11).

At site two, catchability was significantly correlated with the number of microsites used (r^2 =-0.39, p = 0.003). The type of microsite used (log, board or a mixture) did not significantly influence catchability at either site two (F = 1.63, p = 0.2) or at site four (F = 0.68, p = .5).

Microhabitat

Almost all captures of animals were made on the stabilized dune. The only exceptions were the occasional yearling or hatchling found under debris on the beach or animals found at the forest edge. Animals occasionally climbed shrubs to evade capture and twice males were seen basking in trees. However the majority of the data collected refers to animals captured under cover.

Figure 10. Comparison of number of captures of males (open square), females with known nest site (closed circle), females with no known nest site (open circle) and yearlings (open triangle) during three time periods. Analyses of variance were conducted separately on each time period. Data points with the same letter under them do not differ significantly (Scheffe's multiple comparison, $p < 0.05$)

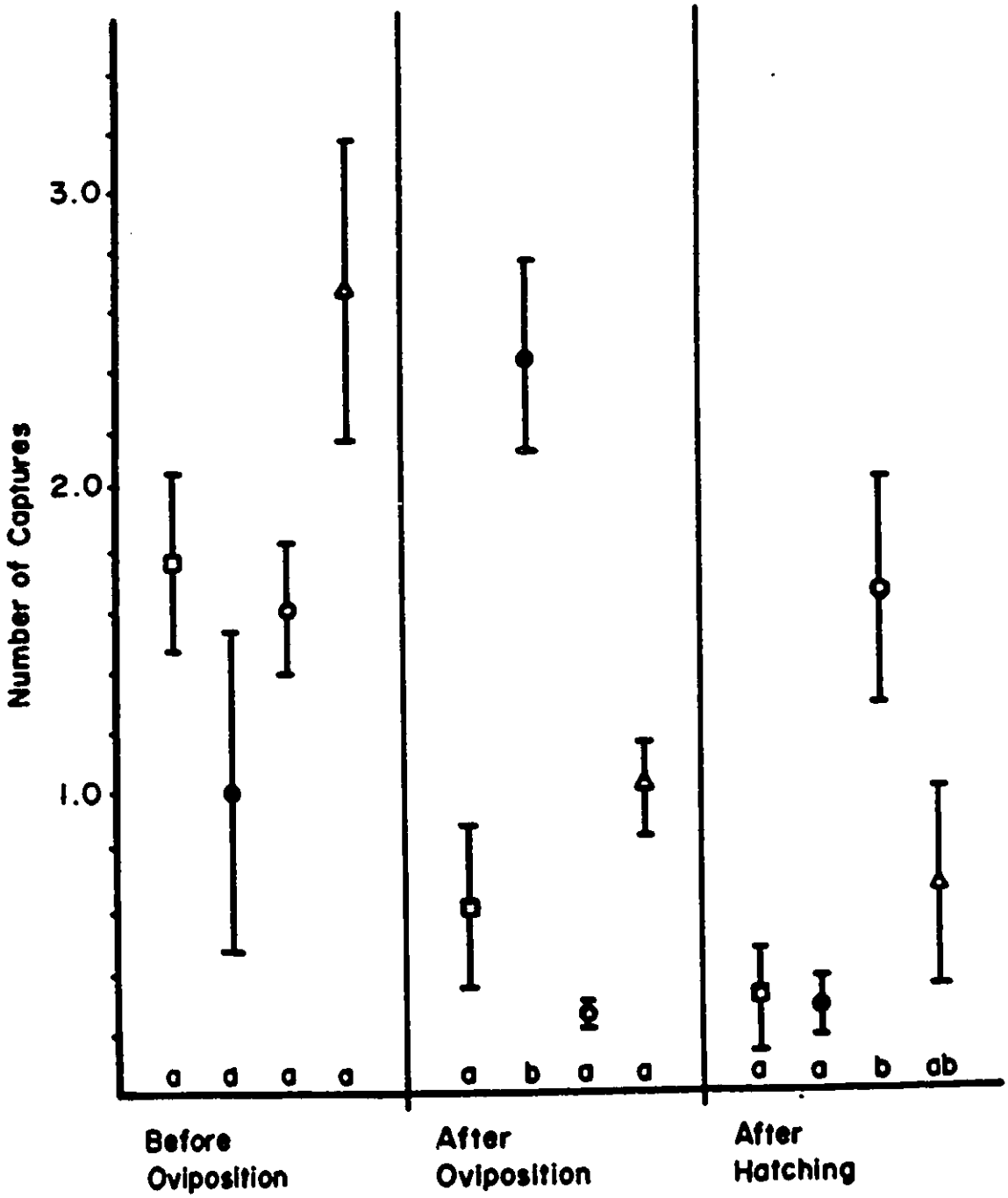
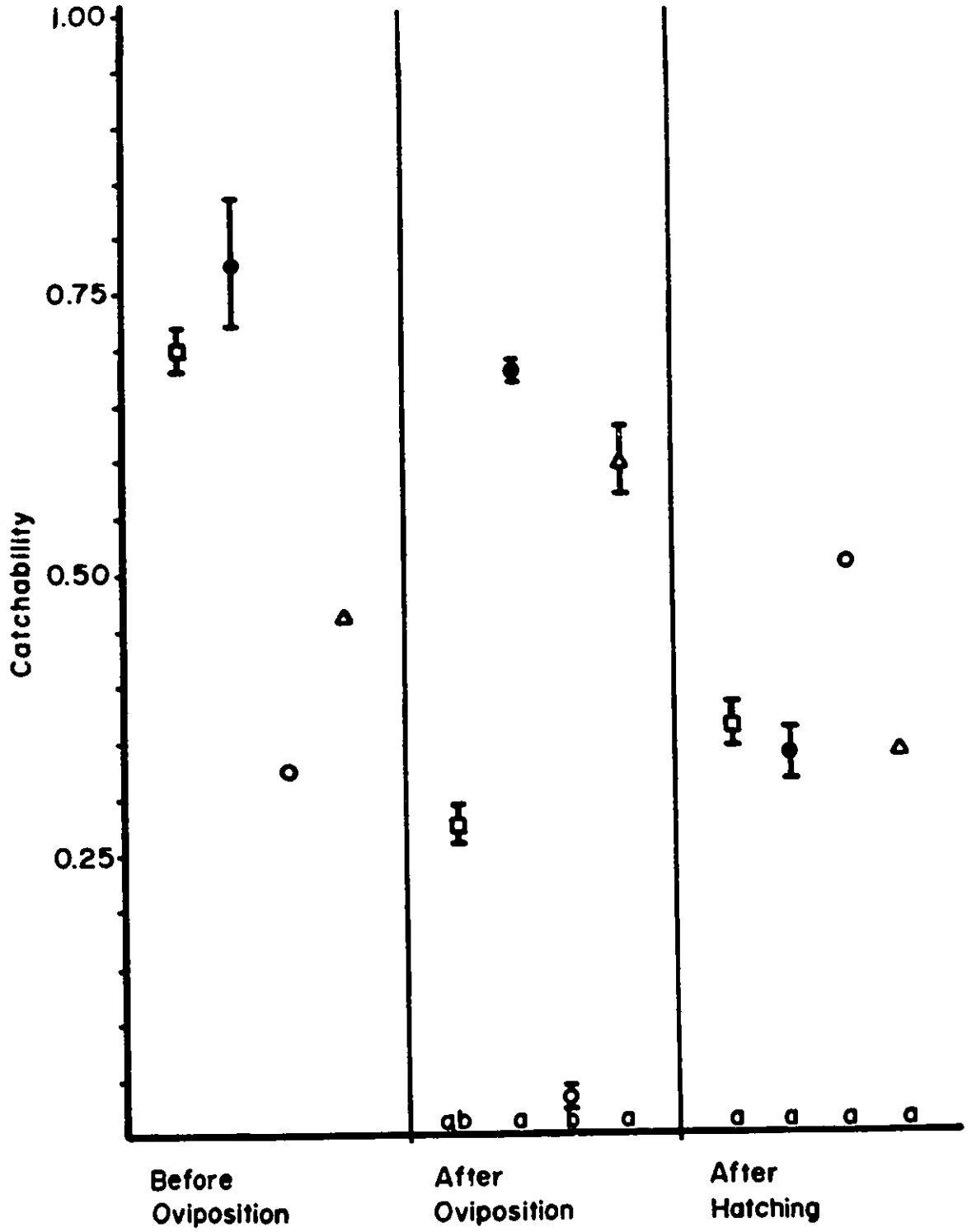

Number of Captures
3.0
2.0
1.0
a a a a
a b a a
a a b ab
Before Oviposition
After Oviposition
After Hatching

Figure 11. Comparison of catchability of males (open square), females with known nest site (closed circle), females with no known nest site (open circle) and yearlings (open triangle) during three time periods. Kruskal-Wallis test conducted on "before oviposition" data. Analyses of variance were conducted separately on remaining time periods. Data points with the same letter under them do not differ significantly (Scheffe's multiple comparison, $p < 0.05$)


1.00
0.75
0.50
0.25
Catchability
ab
a
b
a
a
a
a
a
Before Oviposition
After Oviposition
After Hatching

Microsites differed widely in use by animals. Some microsites that appeared perfectly suitable were apparently never, or rarely, used, while others were occupied by up to 16 different animals throughout the season and were rarely unoccupied.

Microsites were considered artificial if they showed signs of having been cut, painted, glued or nailed. Natural and artificial microsites were compared on the basis of surface area, thickness, per cent shade, and distance to nearest neighbour (Table 27). Natural debris had greater surface area and thickness than artificial debris but did not differ otherwise.

Surface area and thickness were used as covariates in an ancova comparing natural and artificial debris for total number of animals found (excluding hatchlings), total number of males, females, yearlings, or hatchlings, or presence of nest sites. Natural debris harboured significantly more females, hatchlings and nest sites, but only when surface area and thickness effects were not removed (Table 28).

The frequency of microhabitat classes is displayed in figure 12. Microhabitat classes were compared for surface area, thickness, shadedness and distance to nearest neighbour (Table 29). Classes were also compared on the basis of numbers of different types of animals found both in total and during different times in the summer. Because of the large number of tests done, a significance level of $p < 0.002$ is

Table 27. Comparison of natural and artificial microsites using manova on surface area (cm^2), thickness (cm), shadedness (per cent shade) and distance to nearest neighbour (m). Standard errors are given in parentheses.

	N	SURFACE AREA	THICKNESS	SHADE	TO DISTANCE NEIGHBOUR
NATURAL	35	5938	15.08	37	4.86
		(1047)	(1.69)	(5)	(0.70)
ARTIFICIAL	31	2364	3.42	58	3.20
		(357)	(0.60)	(5)	(0.56)
F		5.21	30.38	2.02	2.74
p		0.026	0.0001	0.16	0.10
MANOVA		F = 8.96		p < 0.0001	

Table 28. Comparison of natural and artificial microsites for numbers of animals found, using surface area and thickness as covariates. Model F and p values refer to the overall significance level of the test. Corrected F and p values refer to the significance level when the effects of surface area and thickness are removed. Standard errors are given in parentheses under the mean number of animals found at each microsite.

	NATURAL MICROSITES	ARTIFICIAL MICROSITES	MODEL F	p	CORRECTED F	p
YEARLINGS AND ADULTS	2.51 (0.31)	2.34 (0.49)	1.95	0.1	0.08	0.8
MALES	0.51 (0.10)	0.80 (0.19)	1.19	0.3	0.26	0.6
FEMALES	1.04 (0.20)	0.88 (0.23)	2.97	0.039	0.15	0.7
YEARLINGS	0.80 (0.15)	0.56 (0.14)	1.09	0.4	0.02	0.9
HATCHLINGS	1.56 (0.47)	0.54 (0.17)	3.63	0.018	0.03	0.9
NEST PRESENCE	0.13 (0.05)	0.08 (0.04)	3.75	0.015	0.20	0.7

Figure 12. Frequency of microhabitat classes at sites two (top) and four (bottom).

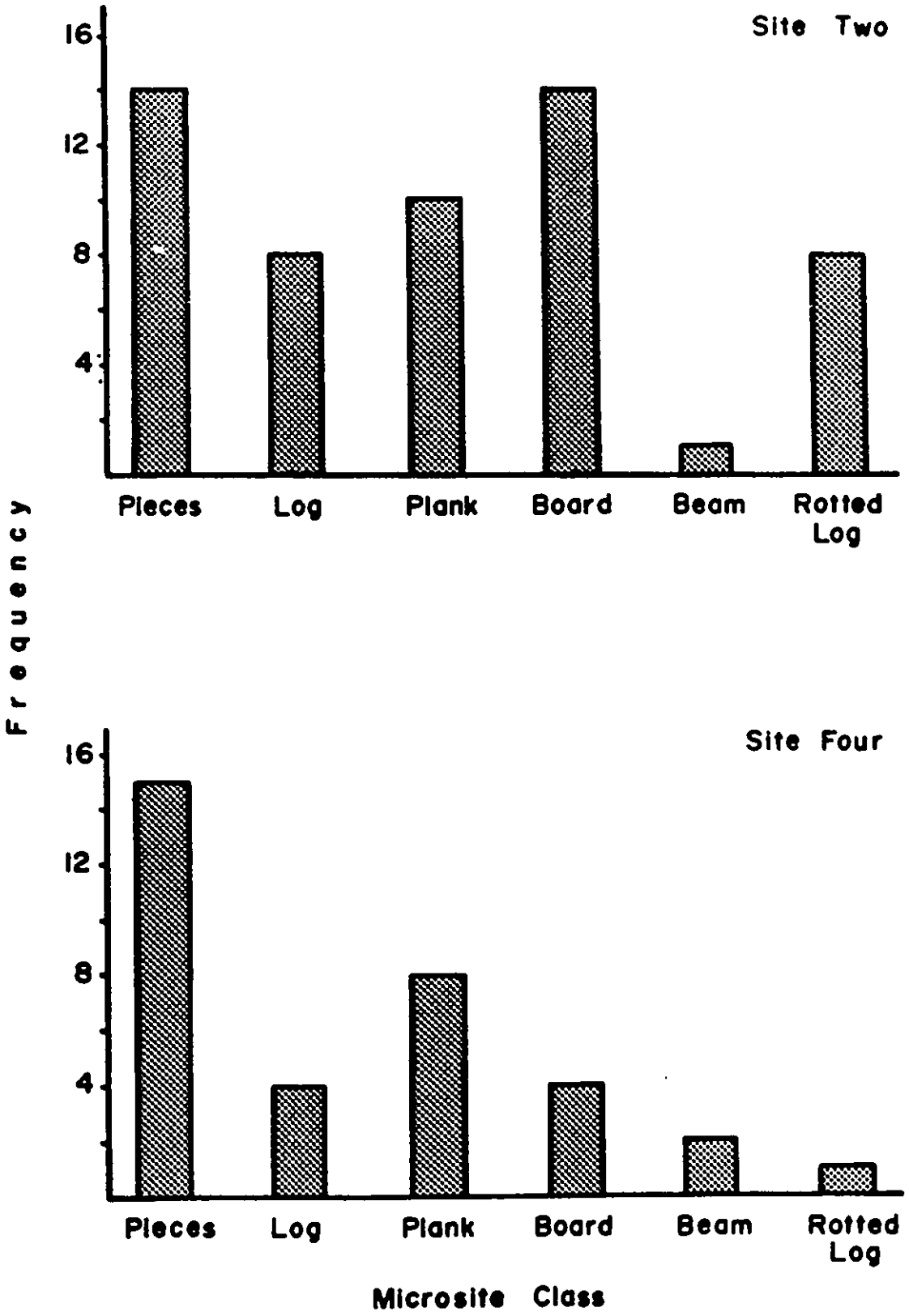

Site Two
16
12
8
4
Pieces
Log
Plank
Board
Beam
Rotted Log
Frequency
Site Four
16
12
8
4
Pieces
Log
Plank
Board
Beam
Rotted Log
Microsite Class

Table 29. Comparison of the microsite classes on the basis of surface area (cm^2), thickness (cm), shadedness (per cent shade) and distance to nearest neighbour (m). Standard errors are given in parentheses.

	N	SURFACE AREA	THICKNESS	SHADE	DISTANCE TO NEIGHBOUR
PIECES	17	3251	11.53	37	5.61
		(1017)	(2.07)	(7)	(1.28)
LOGS	10	10944	20.20	38	4.46
		(2329)	(3.23)	(13)	(0.98)
PLANKS	12	2517	3.63	63	2.86
		(600)	(0.52)	(9)	(0.77)
BOARDS	14	2139	1.93	55	3.56
		(557)	(0.41)	(6)	(0.92)
BEAMS	2	3625	14.00	10	3.32
		(2050)	(2.00)	(0)	(1.28)
ROTTED	7	5387	15.90	37	4.73
LOGS		(1694)	(3.69)	(10)	(1.16)
x^2		23.75	34.16	10.84	----
F		----	----	----	0.82
p		0.0002	0.0001	0.5	0.055

required to keep alpha < 0.05. None of the comparisons show significant differences (Appendix C).

Average linkage cluster analysis of microsites, using surface area, thickness, shadedness and distance to nearest neighbour, led to the acceptance of eight clusters (Figure 13; Table 30). Clusters were compared on the basis of numbers of different types of skinks found both in total and during different times in the summer. As above, $p < 0.002$ was required for significance. The only significant comparison was that after the eggs hatched, females significantly preferred microsites from cluster seven over those from clusters one, two or three ($F = 5.32$, $p < 0.0001$) (Appendix D).

Finally, I examined the characteristics of those microsites at which nests were found and compared them to those where nests were not found (Table 31). Nine microsites had nests and sixty-six did not. The only significant difference found was that nest sites averaged greater surface area than other sites.

Males, females and yearlings were all found to significantly prefer sites at which nests were found over sites at which nests were not found (Table 32).

During the breeding period females alone showed a significant preference for sites at which nests were later found (Table 33) although during the time that females were gravid, both males and females significantly preferred nest

Figure 13. Dendrogram from average linkage cluster analysis on microsites.

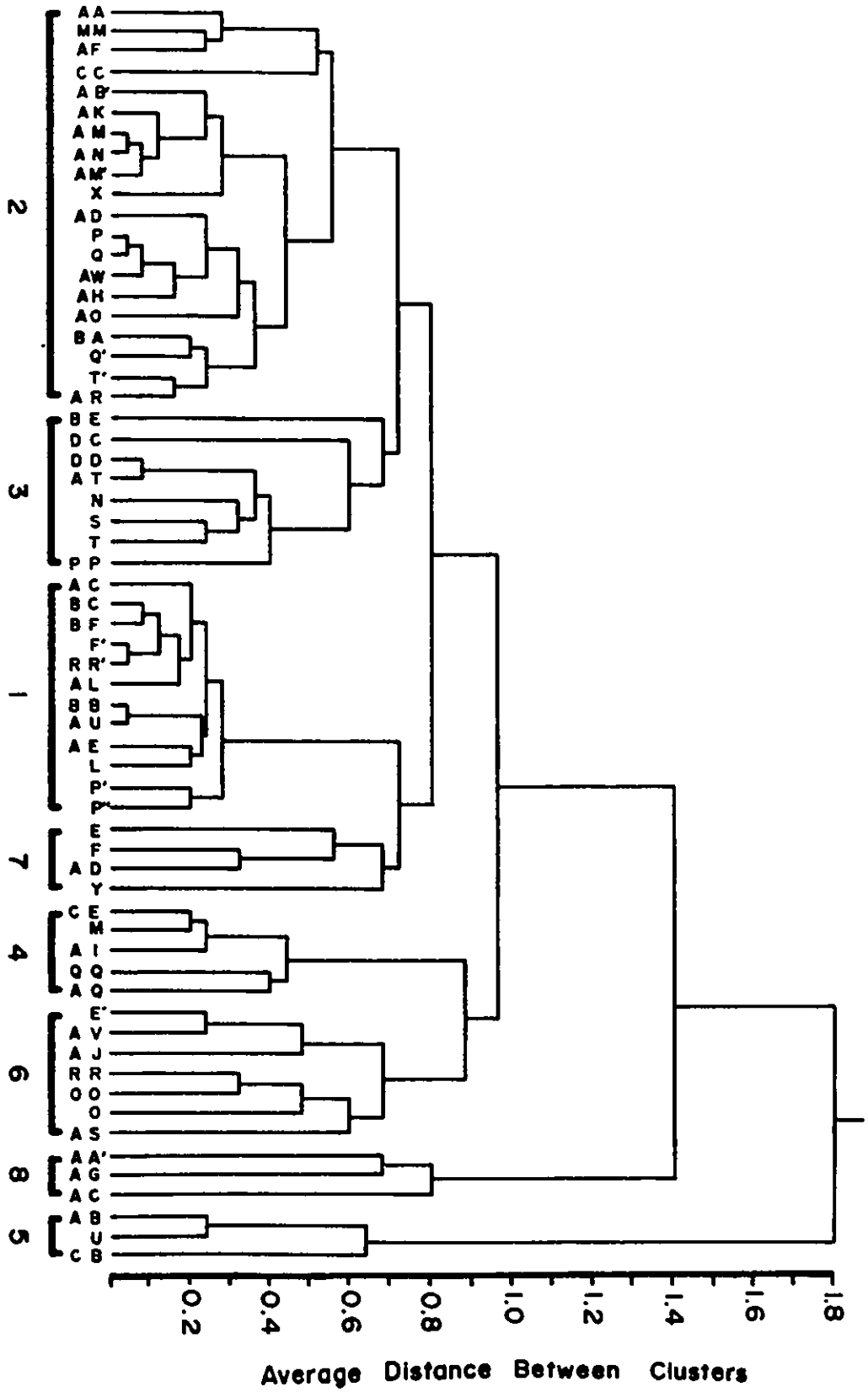

2
3
1
7
4
6
8
5
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
Average Distance Between Clusters

Table 30. Analysis of the variance among eight clusters of microsites for physical characteristics. Standard errors are given in parentheses. Means with different superscript letters differ significantly (Scheffe's multiple comparison, $p < 0.05$).

CLUSTER	N	SURFACE AREA	THICKNESS	SHADE	DISTANCE TO NEIGHBOUR
1	11	2046 ^{ab}	2.87 ^{a}	85 ^{a}	1.62 ^{a}
		(318)	(0.45)	(2)	(0.31)
2	20	1856 ^{a}	5.95 ^{a}	27 ^{bd}	2.98 ^{a}
		(264)	(0.92)	(4)	(0.44)
3	8	2459 ^{ab}	2.22 ^{a}	49 ^{bce}	8.86 ^{b}
		(948)	(0.71)	(7)	(0.64)
4	5	5617 ^{bc}	19.20 ^{bd}	8 ^{d}	1.78 ^{a}
		(1031)	(1.77)	(2)	(0.59)
5	3	20028 ^{d}	31.00 ^{c}	15 ^{bd}	5.36 ^{ab}
		(1529)	(3.06)	(6)	(1.85)
6	7	3593 ^{ab}	24.14 ^{cd}	65 ^{ac}	5.38 ^{ab}
		(517)	(1.37)	(9)	(1.21)
7	4	8461 ^{c}	10.13 ^{ab}	73 ^{ae}	1.49 ^{a}
		(1699)	(3.26)	(8)	(0.52)
8	3	3867 ^{abc}	9.83 ^{ab}	20 ^{bcd}	17.02 ^{c}
		(1464)	(5.07)	(15)	(1.52)
F		50.00	40.16	20.89	28.56
p		0.0001	0.0001	0.0001	0.0001

Table 31. Analysis of variance for physical characteristics of sites where nests were found versus those where nests were not found. Variables used are surface area (cm^2), thickness (cm), shade (per cent shaded), and distance to nearest neighbour (m). Standard errors are given in parentheses.

	SURFACE AREA	THICKNESS	SHADE	DISTANCE TO NEIGHBOUR
NEST PRESENT	9717 (2748)	13.21 (3.48)	34 (11)	3.39 (1.21)
NEST ABSENT	3591 (560)	9.33 (1.29)	47 (4)	4.37 (0.54)
F	11.80	1.05	1.17	0.43
p	0.0011	0.3	0.3	0.5

Table 32. Comparison of microsites with nests versus those without nests for numbers of animals found throughout the spring and summer. Standard errors are given in parentheses.

	MALES	FEMALES	YEARLINGS	ALL
NEST PRESENT	1.56 (0.60)	3.22 (0.57)	1.44 (0.58)	6.44 (1.55)
NEST ABSENT	0.61 (0.10)	0.76 (0.15)	0.61 (0.10)	2.08 (0.23)
F	7.67	30.89	6.35	26.47
p	0.007	0.0001	0.014	0.0001

Table 33. Comparison of microsites with nests versus those without nests for numbers of animals found during the breeding period (May 16 - June 12). Standard errors are given in parentheses.

	MALES	FEMALES	YEARLINGS	ALL
NEST PRESENT	0.67 (0.37)	0.67 (0.29)	0.22 (0.45)	1.56 (0.60)
NEST ABSENT	0.27 (0.07)	0.20 (0.05)	0.26 (0.07)	0.77 (0.14)
F	3.08	6.92	0.03	3.29
p	0.08	0.01	0.86	0.07

sites (Table 34). However, during nesting, only females preferred nest sites significantly over other sites (Table 35). Male numbers were too low to show a significant effect. Finally, after the eggs hatched, males, females and hatchlings were all found to prefer nest locations (Tables 36 and 37). It is notable that although yearlings did not show a significant preference during any particular time period, their preference for nests sites was only significant over the whole field season.

Table 34. Comparison of microsites with nests versus those without nests for numbers of animals found when females were gravid (June 13 - July 11). Standard errors are given in parentheses.

	MALES	FEMALES	YEARLINGS	ALL
NEST PRESENT	0.67 (0.24)	1.22 (0.43)	0.77 (0.46)	2.67 (0.94)
NEST ABSENT	0.20 (0.05)	0.18 (0.06)	0.20 (0.06)	0.59 (0.12)
x^2	----	14.43	1.98	9.10
F	7.76	----	----	----
p	0.0068	0.0002	0.16	0.0026

Table 35. Comparison of microsites with nests versus those without nests for numbers of animals found during the nesting period (July 12 - August 1). Standard errors are given in parentheses.

	MALES	FEMALES	YEARLINGS	ALL
NEST PRESENT	0.33 (0.17)	1.00 (0.24)	0.33 (0.24)	1.89 (0.39)
NEST ABSENT	0.14 (0.04)	0.15 (0.08)	0.08 (0.03)	0.41 (0.08)
X^2	----	----	2.21	----
F	2.3	28.74	----	32.59
p	0.14	0.0001	0.13	0.0001

Table 36. Comparison of microsites with nests versus those without nests for numbers of animals found after hatching (August 2 - September 30). Standard errors are given in parentheses.

	MALES	FEMALES	YEARLINGS	ALL
NEST PRESENT	0.33 (0.17)	1.44 (0.47)	0.33 (0.33)	2.11 (0.82)
NEST ABSENT	0.10 (0.04)	0.36 (0.08)	0.06 (0.04)	0.52 (0.11)
X^2	----	----	0.77	5.96
F	4.56	14.85	----	----
p	0.036	0.0002	0.38	0.015

Table 37. Comparison of microsites with nests versus those without nests for numbers of hatchlings. Standard errors are given in parentheses.

	HATCHLINGS	F	p
NEST PRESENT	4.11 (1.65)	9.69	0.0019
NEST ABSENT	0.80 (0.22)		

Discussion

Spatial distribution

In total, as well as within age and sex classes, skinks aggregated to a significant degree. It should be noted that the analysis used microsites (or groups of microsites) as units of location. This does not take into account the distribution of the microsites themselves. Therefore, the results should be interpreted as indicating that animals cluster with respect to the location of microsites. The increase in the number of significant effects when groups of microsites were used suggests that clumping of microsites increases the overall aggregation of the skink population.

Microsites included in the analysis were locations where at least one animal had been found at some time during the summer, or which because of their size, appeared to be highly suitable sites although no animal had ever been captured there. The extreme popularity of some microsites suggests that there is a great deal of variability in the suitability of these microsites. Unfortunately, an insufficient number of nests was found to test the hypothesis that nest sites are aggregated. However, nests were often found together.

There are a variety of possible proximate causes of spatial aggregation. For example, at birth, skinks are spatially aggregated because several eggs are laid in a single nest. In addition, several females may nest at the same microsite (Noble and Mason, 1933; Fitch, 1954; pers.

obs.). Thus, aggregated skinks may be brood mates. However, it is unlikely that this is strictly true because hatchlings and yearlings are quite mobile (Fitch, 1954; this study). Aggregation of siblings could also lead to inbreeding. However, sexes may disperse differentially such that aggregated skinks could be sisters (or brothers). This hypothesis would require several years of data to test.

Cooper and Garstka (1987) demonstrated that Eumeces laticeps aggregate prior to hibernation under laboratory conditions of excess shelter sites. Hibernacula of E. fasciatus have also been found (Hamilton, 1948; Neill, 1948; Fitch, 1954). Thus, summer aggregation may simply reflect remnants of winter aggregations. This hypothesis seems unlikely because the skinks were aggregated throughout the summer despite a high turnover of animals at particular microsites.

In addition, skinks may aggregate because of a shortage of suitable microsites. Addition of excess microsites would test this possibility. Finally, that skinks may use conspecifics as cues to the suitability of microhabitat could be tested using the protocol of M'Closkey et al. (1990c). This would involve introduction of animals to both occupied and unoccupied microsites. Such an experiment could be particularly informative if conducted on gravid females just prior to oviposition because they normally exhibit site tenacity and therefore experimental effects would be easier

to detect.

The association found between males and females during the breeding period suggests that at least some of the aggregation among animals relates to mating behaviour and other social interactions.

The observation that more than one male may make use of the same microsite (though not necessarily simultaneously) suggests that males do not defend territories although they may defend individual space (Kaufmann, 1983) or access to females.

Residence and Movement

The results of the comparison of the ratio of residents to non-residents to that predicted by the zero truncated binomial (Table 20), suggest that the majority of animals that were captured only once were indeed resident in the sites. The exceptions were among the yearlings, males at site one and females at site four. There were truly non-resident yearlings in all sites. Non-resident males were found only at site one and non-resident females were found only at site four. Given this information, the interaction between the residence ratio and sex (Table 21) implies that males were more likely to be captured only once by chance than were females. This result is likely a reflection of the microsite tenacity exhibited by females while they are brooding and supports the idea of males becoming secretive

after the breeding period. The results on movement must be interpreted cautiously because movement outside of sites could not be detected, nor could use of subterranean or arboreal habitats.

Some females moved long distances prior to oviposition and in some cases returned after eggs hatched, suggesting that some females may nest in locations that they do not use during the rest of the season. In support of this, several females disappeared during the nesting period and reappeared afterward. Presumably, these females also found microsites that they used only for nesting, but these nests were not located either because they were inside logs, in other inaccessible places, or outside the study site. Furthermore, those females (with one exception), whose nest location was known, were only found at that location during the nesting period or shortly before or after that time. I found that in some cases the microsite that some females abandoned served as another female's nest site.

I can only speculate on the significance of changes in location. Perhaps there is a dominance hierarchy of females so that subordinate females are displaced and move. It is possible that there is some unknown factor that causes females to move -- such as evasion of parasites or as a dispersal/outbreeding strategy. Females may abandon hatchlings so as to avoid cannibalism (Vitt and Cooper, 1986). Movements before and after nesting have not

previously been reported in the five-lined skink. However, Urosaurus ornatus leave their home range to oviposit and return shortly thereafter (M'Closkey, pers. comm.). Fox (1983) studied home range use in juvenile Uta stansburiana (Iguanidae) and found a tendency to shift home ranges when the opportunity was provided by experimental removal of adults.

It is also possible that females moved before laying their eggs because they were disturbed in the course of this research. How capture and handling affected the behaviour of the skinks can not be known, but animals were often found at the same microsite over several consecutive censuses.

Capture Statistics

Catchability is commonly calculated to test the assumption of equal catchability required by the Jolly-Seber method of population estimation (Krebs, 1989; Part One). Because catchability is a product of the interaction between the investigator and the animals studied, catchabilities measured in different studies are not comparable. However, comparison of catchabilities within a study may reveal biases in the sampling method such as when one sex is easier to catch than another.

The difference between study sites for catchability and residence time largely reflects the difference in the number of censuses conducted. Sites one and three were each censused six times and do not differ for any of the capture variables. Females whose nest location was known (n = 7) differed significantly from those with no known nest location (n = 23) in the following ways. During the nesting period, females with known nest locations had more captures and greater catchability than those without. The reverse was true after hatching. Catchability did not differ

significantly after hatching but only three females with known nests were caught after hatching and therefore catchability scores could not be calculated for the other five females. Because of low numbers, a significant result almost impossible to achieve. These results support the notion that females change locations to nest and remain at the nest site while brooding.

Microhabitat

Five-lined skinks may make use of a wide variety of different types of microhabitat including wood (Fitch, 1954), trees (Fitch and von Achen, 1977), rock piles (Fitch, 1954) and rock outcrops (pers. obs.). In this study the majority of animals were found under pieces of wood.

Approximately equal numbers of natural and artificial microsites were found in the park. Aside from a slight preference for nests and hatchlings to be found at natural microsites, artificial microsites harboured as many animals as natural ones, even when differences in surface area and thickness were not taken into account. Thus, artificial, woody, debris makes up a significant component of the available microhabitat and park staff should be discouraged from removing it.

The five-lined skinks did not appear to differentiate between different classes of debris (pieces, logs, planks, boards, beams, or rotted logs) even though debris differed in

surface area and thickness. Cluster analysis also did little to reveal preferences except that after eggs hatched, females preferred debris with intermediate surface area and thickness over smaller, thinner debris. Comparison of the eight clusters did reveal that there is a general relationship between surface area and thickness of debris. Clusters with large mean surface area tended to have the greatest mean thickness. Yet, skinks would be expected to prefer thin debris with large surface area which would allow thermoregulation under cover. Therefore, skink microsite selection may be a tradeoff between surface area and thinness.

The presence or absence of a nest at a microsite was a good predictor of the presence or absence of animals throughout the season. This may be a result of females choosing nest sites with qualities that are generally preferred by all animals at all times, or it may be a result of animals congregating at potential nest locations for social reasons. That adults showed greater preference for nest locations than did yearlings, suggests that social interactions may be important. Yearlings may be excluded by adults or they may not participate in social interactions.

The trend throughout the seasons suggests that females increase their preference for potential nest locations from emergence until nesting time. Males showed this preference at about the time that females became noticeably gravid.

This suggests that males may seek females at potential nest locations and then remain with them until oviposition. This result implies mate guarding. Vitt and Cooper (1985) report mate guarding in E. laticeps. Once the eggs were laid, the number of males found decreased and significant effects are no longer seen.

Microsites at which nests were found differed in having significantly greater surface area than microsites with no nest. However, the cluster of microsites with the greatest surface area was not preferred over other microsites. This suggests that other factors are involved. Because E. fasciatus readily dehydrates (Fitch, 1954) and is ectothermic, I suggest that soil moisture and temperature may be important and that soil moisture under debris with large surface area may be more constant than under smaller debris.

The continuous preference of females for potential nest locations appears to contradict the earlier result in which females changed location in order to nest. However, recall that other females sometimes recolonized abandoned microsites.

Conclusion

The aggregated distribution of the five-lined skink supports the hypothesis that it is not territorial (Fitch, 1954). However, the proximate cause of aggregation behaviour is unclear and requires further study. The five-lined skink is a good candidate for testing the conspecific cuing hypothesis (Kiester and Slatkin, 1974).

At Point Pelee, Eumeces fasciatus makes use of a wide variety of shapes and sizes of debris. Throughout its range it can be found in open sandy fields, near marshes, on rock outcrops, or on trees at the edge of a woods (Seburn, unpublished data). Comparison of E. fasciatus microhabitat preferences in sympatry and in allopatry with E. laticeps and E. inexpectatus is likely to reveal habitat segregation (Diamond, 1986). Niche overlap models would predict a reduction in niche breadth in sympatric populations as compared to allopatric populations (MacArthur and Levins, 1967) although the reverse is also possible (Rosenzweig, 1989).

GENERAL CONCLUSION

The five-lined skink is a difficult animal to study in the field because of its secretive habits and its quickness at moderate temperatures. However, Point Pelee appears to be an ideal place to study the skink (provided the problem of site disturbance can be resolved) because the habitat provides numerous locations where animals are accessible to capture before they become active in the early morning. These locations can be thought of as analogous to trap stations and artificial supplementation of such debris may prove a useful tool in future studies.

Studies of the five-lined skink can be used to address a number of questions which are of interest to ecologists. Because the skinks occupy an intermediate successional stage, the effects of disturbances such as visitor use, or maintenance and construction of boardwalks and buildings can be studied. If telemetry techniques can be developed for use with skinks, this will provide valuable data on activity and spatial behaviour for comparison with iguanid lizards. In addition, egg retention times of skinks at Point Pelee was greater than those in Kansas suggesting that further study may provide insights into the evolution of ovoviparity and the relationship between brooding behaviour and viviparity.

The data suggest that this species is not territorial. This is probably because it would be difficult for the skinks to detect intruders, given their secretive behaviour (Fitch,

1954; Stamps, 1977). By a similar argument, it is likely that the skinks are polygynandrous. Successful mate guarding would be difficult unless females are only sexually receptive for a short period of time. Nonetheless, E. fasciatus are sexually dimorphic. Thus, an opportunity exists to evaluate the relationship between territoriality, mating system and sexual dimorphism in this species (Stamps, 1977, 1983).

The variation in density of animals associated with variation in density of debris and the variety of habitats occupied throughout the range provide several opportunities for study. There is a natural analog for studies of changes in dominance behaviour with increasing density (Carpenter, 1967). Variation in habitat structure may allow for differences in the potential for territoriality and therefore in mating system (Emlen and Oring, 1977).

Finally, the existence of three closely related species which differ in the degree of sexual dimorphism allows the possibility to study the evolution of sexual dimorphism and its relation to niche differences between the species (Stamps, 1983).

SUMMARY

1. The objective of this study was to examine the population ecology of the five-lined skink (Eumeces fasciatus).

2. This was undertaken in a mark-recapture study of a population at Point Pelee National Park in which population structure, mating system, spacing patterns and microhabitat preferences were examined.

3. Prior to the hatching period, yearlings, adult males, and adult females each made up one third of the population. The population was more than doubled by hatchlings.

4. Compared with a population studied in Kansas (Fitch, 1954), the Point Pelee population emerged from hibernation up to two weeks later. In addition gravid females retained their eggs 8-22 days longer, and brooded them up to 19 days less. This may be an adaptation to the shorter reproductive season in Ontario.

5. Females made movements of up to 68 m before and after nesting. Some females returned to their original site

of capture after the eggs hatched. Females whose nest site was known tended to only be caught during the nesting period while females with no known nest site tended to be caught before or after nesting but not during. These results suggest that females nest in locations that differ from where they spend the rest of their time and that while nesting they do not leave the nest.

6. The five-lined skinks were sexually dimorphic for head and tail width but did not differ in svl. Females lost up to 5 g at oviposition and their weight remained low, relative to males until after the eggs hatched.

7. Individuals within the population aggregated spatially. This implies that skinks are not territorial.

8. Males and females associated significantly only during the breeding period.

9. A zero-truncated binomial model was used to determine how many resident animals would only be captured once, by chance.

10. Yearlings and adult males were more likely to be

non-resident than adult females.

11. Artificial woody debris made up a large component of the microhabitat available to and used by the skinks.

12. Nests were found at microsites that averaged significantly greater surface area than microsites where they were not found.

13. The presence of a nest at a microsite during the nesting period was the best predictor of microsite preference throughout most of the spring and summer.

14. The aggregated distribution of animals in conjunction with their widely foraging habits make a polygynandrous mating system likely. However, some mate guarding was seen, so the mating system may be variable.

15. The greater relative head width of males may be a result of sexual selection. Although sexual selection is often associated with territorial species, it may also occur in species where one sex invests more in parental care than the other (Trivers, 1972). The movement patterns, brooding behaviour, and reduced feeding in female five-lined skinks support the hypothesis that females invest more in offspring than males do.

APPENDIX A

Calibration of Scales

Two scales were used to collect data on lizard weights. Adults and yearlings were weighed using a Pesola 50 g scale. Hatchlings were weighed using a Pesola 10 g scale. Because of a discrepancy between the two scales over the weight of the weighing bag the two scales were calibrated against a set of standard brass weights.

The Pesola 50 g scale was checked using standard weights of 1, 2, 5, 10 and 20 g. The Pesola 10 g scale was checked using standard weights of 0.2, 0.4, 0.5, 0.6, 1, 2, 5, and 10 g. In addition the weighing bag was weighed on a Mettler AC100 balance. Measured weights for the two scales were regressed against the standard weights and a calibration equation was determined.

A plot of the data showed the relationships to be approximately linear. The expected regression line for an accurate scale is the line with slope one and intercept zero. The regression line for the Pesola 10 g did not differ significantly from this. The regression line for the Pesola 50g scale differed significantly in both slope and intercept ($p < 0.05$).

The correction equation for the Pesola 50g scale was:

$$\text{STANDARD} = 0.937 + 0.934(\text{MEASURED VALUE})$$

This correction was applied before subtracting the weight of the weighing bag.

APPENDIX B

A Null Model of The Ratio of Residents to Non-Residents

Even if all animals in a site are resident, one would expect by chance that some of these animals will only be caught once. It would therefore be useful to determine what the expected number of such animals is and to test the significance of departures from that expected number. In order to do so it is necessary to assume that there is some number p which represents the probability that an animal will be captured in a census. It is assumed that p is a characteristic of the interaction between the investigator, the habitat and the population and does not vary among individuals. If this is the case, then the distribution of capture frequencies will be binomial and the expected ratio of residents to non-residents can be calculated after p has been determined. In reality, the number of animals with zero captures is unknowable and therefore a zero truncated binomial (Johnson and Kotz, 1971) must be substituted for the usual binomial. The zero truncated binomial is of the following form.

$$C_r = \frac{N\,[n!/r!(n-r)!]p^r(1-p)^{n-r}}{1-(1-p)^n}$$

where N is the total number of animals in the site

n is the number of censuses

r is the number of times an animal has been captured in n censuses

C_r is the average number of animals caught r times in n censuses.

The quantity C_r can be estimated by x_r, the actual number of animals caught r times in n censuses. The probability p can then be solved for using the following formulae.

Let

$$A = \sum_{r=1}^{n} C_r$$

then

$$x = A^{-1} \sum_{r=1}^{n} C_r(r)$$

$$= np[1-(1-p)^{n}]^{-1}.$$

This can be solved by the method of successive approximation. Given p, the expected number of non-residents is calculated as the average number of animals caught once in n censuses. The expected number of residents is the sum of C_r for r greater than one. The significance of departures can be tested using a G statistic (Sokal and Rohlf, 1981).

APPENDIX C

Comparison Among Classes of Microsites for the Presence of Skinks

Comparison among six microsite classes for the average number of animals found. Standard errors are in parentheses.

CLASS	N	MALES	FEMALES	YEARLINGS	TOTAL
1	21	0.71	0.81	0.71	2.38
		(0.17)	(0.19)	(0.20)	(0.40)
2	10	0.20	1.80	0.90	3.00
		(0.13)	(0.65)	(0.31)	(0.82)
3	13	1.23	1.31	0.77	3.38
		(0.39)	(0.55)	(0.17)	(0.96)
4	18	0.44	0.56	0.33	1.44
		(0.15)	(0.15)	(0.11)	(0.26)
5	2	3.00	3.00	2.50	9.00
		(2.00)	(3.00)	(2.50)	(7.00)
6	10	0.60	1.10	0.80	2.60
		(0.22)	(0.43)	(0.39)	(0.82)
x^2		10.18	2.86	4.62	5.29
p		0.07	0.7	0.5	0.4

Comparison among six classes of microsites for number of males captured during four different time periods. Standard errors in parentheses.

CLASS	N	BREEDING	GRAVID	BROODING	POST HATCHING
1	21	0.24	0.38	0.10	0.14
		(0.10)	(0.13)	(0.07)	(0.08)
2	10	0.00	0.10	0.00	0.10
		(0.00)	(0.10)	(0.00)	(0.10)
3	13	0.62	0.31	0.38	0.15
		(0.24)	(0.17)	(0.15)	(0.10)
4	18	0.28	0.17	0.11	0.00
		(0.11)	(0.09)	(0.08)	(0.00)
5	2	2.00	0.50	0.50	0.50
		(1.00)	(0.50)	(0.50)	(0.50)
6	10	0.20	0.10	0.20	0.20
		(0.20)	(0.10)	(0.13)	(0.13)
x^2		13.40	0.91	9.37	5.93
p		0.02	0.5	0.1	0.3

Comparison among six classes of microsites for number of females captured during four different time periods. Standard errors are in parentheses.

CLASS	N	BREEDING	GRAVID	BROODING	POST HATCHING
1	21	0.19	0.24	0.29	0.29
		(0.09)	(0.10)	(0.12)	(0.10)
2	10	0.20	0.40	0.50	1.00
		(0.13)	(0.31)	(0.27)	(0.37)
3	13	0.23	0.38	0.23	0.77
		(0.17)	(0.18)	(0.12)	(0.32)
4	18	0.28	0.11	0.17	0.17
		(0.11)	(0.08)	(0.09)	(0.09)
5	2	1.00	2.00	0.50	1.50
		(1.00)	(2.00)	(0.50)	(1.50)
6	10	0.30	0.30	0.10	0.50
		(0.21)	(0.21)	(0.10)	(0.27)
x^2		2.23	3.60	----	----
F		----	----	0.81	7.32
p		0.8	0.6	0.5	0.2

Comparison among six classes of microsites for number of yearlings captured during four different time periods. Standard errors are in parentheses.

CLASS	N	BREEDING	GRAVID	BROODING	POST HATCHING
1	21	0.33	0.19	0.10	0.00
		(0.17)	(0.11)	(0.07)	(0.00)
2	10	0.20	0.30	0.00	0.20
		(0.13)	(0.21)	(0.00)	(0.20)
3	13	0.23	0.31	0.15	0.08
		(0.12)	(0.17)	(0.10)	(0.08)
4	18	0.17	0.11	0.00	0.06
		(0.09)	(0.07)	(0.00)	(0.06)
5	2	0.00	2.00	1.00	1.50
		(0.00)	(2.00)	(1.00)	(1.50)
6	10	0.40	0.30	0.20	0.00
		(0.22)	(0.15)	(0.13)	(0.00)
x^2		1.39	3.86	9.16	10.67
p		0.9	0.6	0.1	0.058

Comparison among six classes of microsites for number of hatchlings captured during four different time periods. Standard errors are in parentheses.

CLASS	N	POST HATCHING
1	21	0.57
		(0.22)
2	10	2.40
		(1.21)
3	13	0.77
		(0.32)
4	18	0.22
		(0.13)
5	2	3.50
		(1.50)
6	10	3.20
		(1.55)
X^2		14.08
p		0.015

APPENDIX D

Comparison Among Clusters of Microsites for Presence of Skinks

Analysis of the variance among eight clusters of microsites for presence of animals. Standard errors are in parentheses.

CLUSTER	N	MALES	FEMALES	YEARLINGS	TOTAL
1	13	0.69	0.62	1.00	2.46
		(0.29)	(0.18)	(0.23)	(0.57)
2	22	0.68	0.82	0.55	2.09
		(0.20)	(0.25)	(0.18)	(0.47)
3	8	0.88	0.75	0.50	2.13
		(0.23)	(0.25)	(0.19)	(0.30)
4	5	1.20	2.80	1.40	5.40
		(0.97)	(1.35)	(0.93)	(2.89)
5	4	0.00	1.25	1.25	2.75
		(0.00)	(0.63)	(0.75)	(1.31)
6	7	0.43	1.00	0.57	2.00
		(0.20)	(0.58)	(0.43)	(0.93)
7	4	1.25	3.00	0.75	5.50
		(0.95)	(1.29)	(0.25)	(2.33)
8	3	1.00	1.00	1.33	4.00
		(0.58)	(1.00)	(0.33)	(1.53)
X^2		5.83	----	----	6.27
F		----	2.42	0.92	----
p		0.56	0.03	0.50	0.50

Analysis of the variance among eight clusters of microsites for presence of males during four time periods. Standard errors are in parentheses.

CLUSTER	N	BREEDING	GRAVID	BROODING	POST HATCHING
1	13	0.31	0.31	0.31	0.00
		(0.17)	(0.17)	(0.13)	(0.00)
2	22	0.45	0.18	0.05	0.05
		(0.14)	(0.09)	(0.05)	(0.05)
3	8	0.25	0.25	0.50	0.13
		(0.16)	(0.16)	(0.19)	(0.13)
4	5	0.60	0.40	0.20	0.20
		(0.60)	(0.24)	(0.20)	(0.20)
5	4	0.00	0.00	0.00	0.00
		(0.00)	(0.00)	(0.00)	(0.00)
6	7	0.00	0.00	0.00	0.43
		(0.00)	(0.00)	(0.00)	(0.20)
7	4	0.50	0.75	0.25	0.25
		(0.50)	(0.48)	(0.25)	(0.25)
8	3	0.33	0.67	0.00	0.33
		(0.33)	(0.33)	(0.00)	(0.33)
X^2		5.05	9.36	13.42	11.74
p		0.7	0.2	0.06	0.1

Analysis of the variance among eight clusters of microsites for presence of females during four time periods. Standard errors are in parentheses. Means with different superscript letters differ significantly (Scheffe's multiple comparison, $p < 0.05$).

CLUSTER	N	BREEDING	GRAVID	BROODING	POST HATCHING
1	13	0.15	0.08	0.08	0.53 [a]
		(0.10)	(0.08)	(0.08)	(0.14)
2	22	0.27	0.27	0.27	0.18 [a]
		(0.12)	(0.09)	(0.12)	(0.11)
3	8	0.25	0.25	0.25	0.13 [a]
		(0.16)	(0.16)	(0.16)	(0.13)
4	5	0.40	1.40	0.60	1.40 [ab]
		(0.40)	(0.87)	(0.40)	(0.60)
5	4	0.00	0.25	0.25	0.50 [ab]
		(0.00)	(0.25)	(0.25)	(0.29)
6	7	0.29	0.14	0.00	0.57 [ab]
		(0.29)	(0.14)	(0.00)	(0.30)
7	4	0.75	0.50	0.75	2.25 [b]
		(0.25)	(0.50)	(0.48)	(0.85)
8	3	0.67	0.33	0.33	0.33 [ab]
		(0.33)	(0.33)	(0.33)	(0.33)
x^2		9.31	4.05	7.25	----
F		----	----	----	5.32
p		0.2	0.8	0.4	0.0001

Analysis of the variance among eight clusters of microsites for presence of yearlings during four time periods. Standard errors are in parentheses.

CLUSTER	N	BREEDING	GRAVID	BROODING	POST HATCHING
1	13	0.31	0.46	0.23	0.00
		(0.17)	(0.18)	(0.12)	(0.00)
2	22	0.23	0.14	0.05	0.05
		(0.11)	(0.10)	(0.05)	(0.05)
3	8	0.25	0.13	0.00	0.13
		(0.16)	(0.13)	(0.00)	(0.13)
4	5	0.00	1.00	0.40	0.60
		(0.00)	(0.77)	(0.40)	(0.60)
5	4	0.00	0.50	0.00	0.50
		(0.00)	(0.50)	(0.00)	(0.50)
6	7	0.14	0.29	0.29	0.00
		(0.14)	(0.18)	(0.18)	(0.00)
7	4	0.50	0.25	0.00	0.00
		(0.29)	(0.25)	(0.00)	(0.00)
8	3	1.33	0.00	0.00	0.00
		(0.88)	(0.00)	(0.00)	(0.00)
x^2		8.89	6.63	7.94	6.81
p		0.3	0.5	0.3	0.4

Analysis of the variance among eight clusters of microsites for presence of hatchlings. Standard errors are in parentheses.

CLUSTER	N	POST HATCHING
1	13	0.23
		(0.12)
2	22	0.82
		(0.25)
3	8	0.75
		(0.41)
4	5	4.60
		(1.96)
5	4	1.50
		(0.96)
6	7	1.57
		(0.90)
7	4	1.50
		(1.19)
8	3	0.00
		(0.00)
X^2		14.86
p		0.038

LITERATURE CITED

Breckenridge, W. J. 1943. The life history of the black-banded skink (Eumeces septentrionalis septentrionalis (Baird)). American Midland Naturalist 29:591-606.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin 76:160-169.

Brown, J. L. 1975. Geographical ecology of desert rodents. Pages 315-341, M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge Massachusetts.

Brown, J. S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs 59(1):1-20.

Bustard, H. R. 1970. A population study of the scincid lizard Egernia striolata in northern New South Wales. Proceedings, Series C, Koninklijke Nederlandse Akademie van Wetenschappen 73(2):186-212.

Cagle, F. R. 1940. Eggs and natural nests of Eumeces fasciatus. American Midland Naturalist 23:227-233.

Camp, C. L. 1923. Classification of the lizards. Bulletin of the American Museum of Natural History 48:289-481.

Carpenter, C. C. 1967. Aggression and social structure in Iguanid lizards. Pages 87-105 in W. W. Milstead, editor. Lizard Ecology: A Symposium. University of Missouri Press, Columbia, Missouri.

Charnov, E. L. 1976. Optimal foraging, the Marginal Value Theorem. Theoretical Population Biology 9:129-136.

Clark, D. R., and R. J. Hall. 1970. Function of the blue tail-coloration of the five-lined skink (Eumeces fasciatus). Herpetologica 26:271-274.

Clutton-Brock, T. H. 1983. Selection in relation to sex. In D. S. Bendall, editor. Evolution from Molecules to Men. Cambridge University Press.

Coakley, J. P. 1980. Post glacial evolution and modern processes at Point Pelee, Lake Erie. Geologic Survey of Canada, Paper 80:10

Cody, M. L. 1966. A general theory of clutch size. Evolution 20:174-184. 154

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. The American Naturalist 102(924):107-147.

Cody, M. L. and J. M. Diamond. 1975. Ecology and evolution of communities. Belknap Press, Cambridge Massachusetts.

Cooper, W. E. Jr. and W. R. Garstka. 1987. Aggregation in the broad-headed skink (Eumeces laticeps). Copeia 1987(3):807-810.

Cooper, W. E. Jr., M. T. Mendonca, and L. J. Vitt. 1986. Induction of sexual receptivity in the female broad-headed skink, Eumeces laticeps, by Estradiol-17 "Beta". Hormones and Behavior 20:235-242.

Cooper, W. E. Jr., M. T. Mendonca, and L. J. Vitt. 1987. Induction of orange head coloration and activation of courtship and aggression by testosterone in the male broad-headed skink (Eumeces laticeps). Journal of Herpetology 21(2):96-107.

Cooper, W. E. Jr. and L. J. Vitt. 1985a. Blue tails and autotomy: Enhancement of predation avoidance in juvenile skinks. Zeitschrift Fuer Tierpsychologie 10:265-276.

Cooper, W. E. Jr. and L. J. Vitt. 1985b. Responses of skinks, Eumeces fasciatus and E. laticeps to airborne conspecific odors: Further appraisal. Journal of Herpetology 19(4):481-486.

Cooper, W. E. Jr. and L. J. Vitt. 1986a. Interspecific odour discriminations among syntopic congeners in scincid lizards (Genus Eumeces). Behaviour 97:1-9.

Cooper, W. E. Jr. and L. J. Vitt. 1986b. Interspecific odour discrimination by a lizard (Eumeces laticeps). Animal Behaviour 34:367-376.

Cooper, W. E. Jr. and L. J. Vitt. 1986c. Lizard pheromones: Behavioural responses and adaptive significance in skinks of the genus Eumeces. In D. Duvall, D. Muller-Schwarze and R. M. Silverstein, editors. Chemical signals in vertebrates 4. Plenum Publishing Corporation.

Cooper, W. E. Jr. and L. J. Vitt. 1987a. Deferred agonistic behavior in a long-lived scincid lizard Eumeces laticeps. Oecologia (Berlin) 72:321-326.

Cooper, W. E. Jr. and L. J. Vitt. 1987b. Intraspecific and interspecific aggression in lizards of the scincid genus Eumeces: Chemical detection of conspecific sexual competitors. Herpetologica 43(1):7-14.

Cooper, W. E. Jr. and L. J. Vitt. 1987c. Ethological isolation, sexual behavior and pheromones in the Fasciatus species group of the lizard genus Eumeces. Ethology 75:328-336.

Cooper, W. E. Jr. and L. J. Vitt. 1988. Orange head coloration of the male broad-headed skink (Eumeces laticeps), a sexually selected social cue. Copeia 1988(1):1-6.

Darwin, C. R. 1871. The Descent of Man, and Selection in Relation to Sex. London: John Murray.

Davies, N. B. and A. Lundberg. 1984. Food distribution and a variable mating system in the dunnock, Prunella modularis. Journal of Animal Ecology 53:895-912.

Deweese, J. E. and J. W. Wright. 1970. A preliminary karyological analysis of scincid lizards. Mammalian Chromosomes Newsletter 11(3):95-96.

Diamond, J. 1986. Evolution of ecological segregation in the New Guinea montane avifauna. Pages 98-125 in, J. Diamond, and T. J. Case, editors. Community Ecology. Harper and Row, Publishers, New York.

Diamond, J., and T. J. Case, 1986. Community Ecology. Harper and Row, Publishers, New York.

Dunn, O. J. and V. A. Clark. 1987. Applied Statistics: Analysis of variance and regression. Second Edition. John Wiley and Sons.

East, K. M. 1976. Shoreline erosion: Point Pelee national Park. National Parks Branch, Ottawa, Ont. 66 p.

Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197(4300):215-223.

Fisher, R. A. 1958. The genetical theory of natural selection. Dover Publications, New York.

Fitch, A. V. 1964. Temperature tolerances of embryonic Eumeces. Herpetologica 20(3):184-187.

Fitch, H. S. 1954. Life history and ecology of the five-lined skink, Eumeces fasciatus. University of Kansas Publications, Museum of Natural History 8(1): 1-156.

Fitch, H. S. 1955. Habits and adaptations of the great plains skink, Eumeces obsoletus. Ecological Monographs 25:59-83.

Fitch, H. S. 1956. A ten-year-old skink? Herpetologica 12:328.

Fitch, H. S. 1981. Sexual size differences in reptiles. University of Kansas Publications, Museum of Natural History 70:1-41.

Fitch, H. S. and P. L. von Achen. 1977. Spatial relationships and seasonality in the skinks Eumeces fasciatus and Scincella laterale in northeastern Kansas. Herpetologica 33:303-313.

Fox, S. F. 1983. Fitness, Home-Range Quality and Aggression in Uta stansburiana. Pages 149-168 in, R. B. Huey, E. R. Pianka and T. W. Schoener, editors. Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge.

Fretwell, S. D., and H. L. Lucus Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical Development. Acta Biotheoretica XIX(1):16-36.

Geist, V. and M. Bayer. 1988. Sexual dimorphism in the Cervidae and its relation to habitat. Journal of the Zoological Society of London 214:45-53.

Halliday, T. R. and P. A. Verrell. 1988. Body size and age in amphibians and reptiles. Journal of Herpetology 22(3):253-265.

Hamilton, W. J. Jr. 1948. Hibernation site of the lizards Eumeces and Anolis in Louisiana. Copeia, 1948:211.

Hasegawa, M. 1984. Effect of brooding on egg mortality in the lizard Eumeces okadae on Miyake-Jima, Izu Islands, Japan. Copeia (1984):497-500.

Howard, R. D. 1978a. Factors influencing early embryo mortality in bullfrogs. Ecology 59:840-871.

Howard, R. D. 1978b. Big bullfrogs in a little pond. Natural History Magazine 88:30-36.

Huey, R. B., E. R. Pianka, and T. W. Schoener. 1983. Lizard ecology: Studies of a model organism. Harvard University Press, Cambridge. 472pp.

Hutchinson, G. E. 1957. Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

Johnson, N. L. and S. Kotz. 1971. Discrete Distributions: Distributions in Statistics. (Probability and Mathematical Statistics Series). Wiley. 328pp.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration -- stochastic model. Biometrika 52:225-246.

Kaufmann, J. H. 1983. On the definitions and functions of dominance and territoriality. Biological Review 58: 1-20.

Kiester, A. R. and M. Slatkin. 1974. A strategy of movement and resource utilization. Theoretical Population Biology 6:1-20.

Kodric-Brown, A. 1986. Satellites and sneakers: opportunistic male breeding tactics in pupfish (Cyprinodon pecosensis). Behavioral Ecology and Sociobiology 19:425-432.

Kodric-Brown, A. and J. H. Brown. 1984. Truth in advertising: the kinds of traits favored by sexual selection. American Naturalist 124(3):309-323.

Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. Ecology 65(3):689-701.

Kotler, B. P. and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics 19:281-307.

Kozlowski, J. 1989. Sexual size dimorphism: a life history perspective. Oikos 54(2):253-255.

Krebs, C. J. 1898. Ecological Methodology. Harper and Row, Publishers, New York. 654pp.

Krebs, J. R. and N. B. Davies. 1981. An Introduction to Behavioural Ecology. Sinauer Associates, Inc. Sunderland, Massachusetts.

Krebs, J. R., J. T. Erichsen, M. I. Webber and E. L. Charnov. 1977. Optimal prey selection in the great tit, Parus major. Animal Behaviour 25:30-38.

Levins, R. 1979. Coexistence in a variable environment. The American Naturalist 114(6):765-783.

Lups, P. and T. J. Roper. 1988. Tooth size in the European badger (Meles meles) with special reference to sexual dimorphism, diet and intraspecific aggression. Acta Theriologica 33(2):21-33.

MacArthur, R. and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101(921):377-385.

MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. The American Naturalist 100(916):603-609.

May, R. M. 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, New Jersey.

May, R. M. and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. Proceedings of the National Academy of Science, USA 69(5):1109-1113.

M'Closkey, R. T. 1978. Niche separation and assembly in four species of Sonoran desert rodents. The American Naturalist 112(986):683-694.

M'Closkey, R. T. 1985. Patterns of microhabitat use and seed collection within populations of heteromyid rodents. Canadian Journal of Zoology 63(2):325-330.

M'Closkey, R. T., R. J. Deslippe, and C. P. Szpak. 1990a. Tree lizard distribution and mating system. Canadian Journal of Zoology 68:in press

M'Closkey, R. T., R. J. Deslippe, C. P. Szpak, and K. A. Baia. 1990b. Ecological correlates of the variable mating system of an iguanid lizard. Oikos 59:in press.

M'Closkey, R. T., C. P. Szpak, and R. J. Deslippe. 1990c. Experimental assessment of factors affecting the distribution of adult female tree lizards. Oikos 59:in press

Milinski, M., and R. Heller. 1978. Influence of a predator on the optimal foraging behaviour of stickleback. (Gasterosteus aculeatus). Nature (London) 275:642-644.

Milstead, W. W. 1967. Lizard ecology: A Symposium. University of Missouri Press, Columbia, Missouri. 300pp.

Neill, W. T. 1948. Hibernation habits of amphibians and reptiles in Richmond County, Georgia. Herpetologica, 4:107-114.

Noble, G. K. 1939. The role of dominance in the social life of birds. Auk 56:263-273.

Noble, G. K. and E. R. Mason. 1933. Experiments on the brooding habits of the lizards Eumeces and Ophisaurus. American Museum Novitates 619:1-29.

Paine, R. T. and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51(2):145-178.

Pianka, E. R. 1975. Niche relations in desert lizards. Pages 292-314 in, M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge Massachusetts.

Pimm, S. L., M. L. Rosenzweig, and W. Mitchell. 1985. Competition and food selection: Field tests of a theory. Ecology 66(3):798-807.

Raxworthy, C. J. 1989. Courtship, fighting and sexual dimorphism in the banded newt, Triturus sittatus ophryticus. Ethology 81:148-170.

Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology 62(2):327-335.

Rosenzweig, M. L. 1989. Habitat selection, community organization, and small mammal studies. Pages 5-21 in D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, editors. Patterns in the Structure of Mammalian Communities. Special Publication of the Museum of Texas Technical University No. 28, Lubbock, Texas.

Sargent, R. C., M. R. Gross and E. P. van den Berghe. 1986. Male mate choice in fishes. Animal Behaviour 34:545-550.

SAS™ Institute Incorporated. 1985. User's Guide: Basics, Version 5 Edition.

SAS™ Institute Incorporated. 1985. User's Guide: Statistics, Version 5 Edition.

Seburn, C. N. L. and D. C. Seburn. 1989. The Geographical Ecology of the Five-lined Skink. Research Report to RCGS.

Shine, R. 1988. The evolution of large body size in females: A critique of Darwin's "Fecundity Advantage" model. The American Naturalist, 131(1):124-131.

Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect. Ecology 63(3):786-796

Sokal, R. L. 1972. Statistical methods in systematics. Biological Review 40:337-391.

Sokal, R. R. and J. F. Rohlf. 1981. Biometry. W. H. Freeman and Company, New York. 859pp.

Somma, L. A. 1985. Notes on maternal behavior and post-brooding aggression in the prairie skink Eumeces septentrionalis. Nebraska Herpetological Newsletter 6(4):9-12.

Somma, L. A. 1987. Alloparental care in the prairie skink, Eumeces septentrionalis: A case of mistaken identity? Nebraska Herpetological Newsletter 8(2):5-8.

Somma, L. A. 1988. Comments on the use of the term "Brooding" to describe parental behaviour in squamate reptiles. Amphibia-Reptilita 9:89-91.

Somma, L. A. 1989a. Oophagus behavior in brooding prairie skinks, Eumeces septentrionalis. Herpetological Review 20(1):3-4.

Somma, L. A. 1989b. Influence of substrate water content on neonate size in the prairie skink, Eumeces septentrionalis. Great Basin Naturalist 49(2):198-200.

Somma, L. A. 1990. A Categorization and Bibliographic Survey of Parental Behavior in Lepidosaurian Reptiles. Smithsonian Herpetological Information Service No. 81.

Somma, L. A. and J. D. Fawcett. 1989. Brooding behavior of the prairie skink, Eumeces septentrionalis, and its relationship to the hydric environment of the nest. Zoological Journal of the Linnean Society 95:245-256.

Southwood, T. R. E. 1978. Ecological Methods. Chapman and Hall, London. 524pp.

Stamps, J. A. 1977. Social behavior and spacing patterns in lizards. Pages 265-334 in, L. Gans and D. W. Tinkle, editors. Biology of the Reptilia, Volume 7. Academic Press, New York.

Stamps, J. A. 1983. Sexual selection, sexual dimorphism and territoriality. Pages 169-204 in, R. B. Huey, E. R. Pianka and T. W. Schoener, editors. Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge.

Stamps, J. A. 1987. Conspecifics as cues to territory quality: A preference of juvenile lizards (Anolis aeneus) for previously used territories. The American Naturalist 129(5):629-642.

Stamps, J. A. 1988a. The effect of body size on habitat and territory choice in juvenile lizards. Herpetologica 44(4):369-376.

Stamps, J. A. 1988b. Conspecific attraction and aggregation in territorial species. The American Naturalist 131(3):329-347.

Strong, D. R. 1986. Density vagueness: Abiding variance in the demography of real populations. Pages 257-268 in, J. Diamond, and T. J. Case, editors. Community Ecology. Harper and Row, Publishers, New York.

Strong, D. R., D. Simberloff, L. G. Abele, and A. B. Thistle. 1984. Ecological Communities: Conceptual issues and the Evidence. Princeton University Press, Princeton, New Jersey.

Sutherland, W. J. 1985. Chance can produce a sex difference in variance in mating success and explain Bateman's data. Animal Behaviour 33:1349-1352.

Taylor, E. H. 1936. A taxonomic study of the cosmopolitan scincoid lizards of the genus Eumeces with an account of the distribution and relationships of its species. University of Kansas Science Bulletin 23:1-643.

Tinkle, D. W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. The American Naturalist 103(933):501-516.

Tinkle, D. W. and R. E. Ballinger. 1972. Sceloporus undulatus: A study of the intraspecific comparative demography of a lizard. Ecology 53(4):570-584.

Tinkle, D. W., H. M. Wilbur and S. T. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55-74.

Trenhaile, A. S. and R. Dumala. 1978. The geomorphology and origin of Point Pelee, southwestern Ontario. Canadian Journal of Earth Sciences 15:963-970.

Trivers, R. L. 1972. Parental investment and sexual selection. Pages 139-179 in B. Campbell editor. Sexual Selection and the Descent of Man. Aldine, Chicago.

Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in Anolis garmani. Evolution 30:253-269.

Vitt, L. J. and W. E. Cooper, Jr. 1985. The evolution of sexual dimorphism in the skink Eumeces laticeps: an example of sexual selection. Canadian Journal of Zoology 64:583-592.

Vitt, L. J. and W. E. Cooper, Jr. 1986. Skink reproduction and sexual dimorphism: Eumeces fasciatus in the southeastern United States, with notes on Eumeces inexpectatus. Journal of Herpetology 20(1):65-76.

Vitt, L. J. and W. E. Cooper, Jr. 1989. Sexual dimorphism of head and body size in an iguanid lizard: Paradoxical results. American Naturalist 133(5):729-735.

Ward, G. and G. J. FitzGerald. 1979. Male aggression and female mate choice in the threespine stickleback, Gasterosteus aculeatus L. Journal of Fish Biology 30:679-690.

Waser, P. M. and R. H. Wiley. 1979. Mechanisms and evolution of spacing in animals. Pages 159-212 in P. Marler and J. G. Vandenbergh. Handbook of Behavioral Neurobiology Volume 3:Social Behavior and Communication. Plenum Press, New York.

Werner, E. E. 1986. Species interactions in freshwater fish communities. Pages 344-358 in, J. Diamond, and T. J. Case, editors. Community Ecology. Harper and Row, Publishers, New York.

Werner, E. E., J. F. Gilliam, D. J. Hall and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64(6):1540-1548.

Werner, E. E., and D. J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58(4):869-876.

Werner, E. E., and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60(2):256-266.

Whitaker, A. H. 1968. The lizards of the Poor Knights Islands. New Zealand Journal of Science 11:623-651.

Whitham, T. G. 1980. The theory of habitat selection: examined and extended using Pemphigus aphids. The American Naturalist 115(4):449-466.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. The American Naturalist 100:687-690.

Wright, J. W. 1973. Evolution of X_1X_2Y sex chromosome mechanism in the scincid lizard Scincella laterale (Say). Chromosoma 43:101-108.

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Seburn, C.N.L., T.A. Dickinson, and S.C.H. Barrett. (1990). Floral instability in Eichhornia paniculata (Spreng.) Solms (Pontederiaceae): I. Stamen Variation in Genotypes from Brazil. Journal of Evolutionary Biology 3:103-123.